THE NUMERICAL RESULTS OF DIVERSE SYSTEMS OF BREEDING, WITH RESPECT TO TWO PAIRS OF CHARACTERS, LINKED OR INDEPENDENT, WITH SPECIAL RELATION TO THE EFFECTS OF LINKAGE[1]

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[1] From the Zoölogical Laboratory of the JOHNS HOPKINS UNIVERSITY.

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I. GENERAL, DEFINITIONS, METHODS

In an earlier paper (JENNINGS 1916) the present author has given formulae for the results of various systems of breeding, with respect to a single pair of characters.[1] When more than one pair are considered, the distribution of characters that Mendelism seemed to give has been greatly modified by the further discovery that characters may be linked. A first and perhaps practically most important step in determining the actual distribution is to deal numerically with two pairs of characters, linked or independent; this is what the present paper undertakes. The problem is to discover formulae which for a given system of breeding will give in later generations the proportions of the different classes of individuals (zygotes) with respect to two pairs of characters, when we know the constitution of the original progenitors. The present paper deals with: random mating; selection with respect to a single character (dominant or recessive); assortative mating with respect to a single character; and self-fertilization. Inbreeding is reserved for separate treatment. Only typical characters, not sex-linked, are dealt with.

(1) DESIGNATION OF FACTORS

The two members of a pair of alternative factors will be designated *A* and *a;* of a second pair, *B* and *b*, the capital letter representing in

[1] Certain points in this earlier paper require mention or correction:
(1) In section (8), page 65, the values given for *AA, aa* and *Aa*, hold for *any* later generation; the constitution of the population does not change with later matings, as stated in the text. This was pointed out to me independently by Dr. C. H. DANFORTH and by Dr. SEWELL WRIGHT. A slip with this correction was enclosed with the reprints distributed. [In the meantime the matter has been fully discussed by WENTWORTH and REMICK (1916).—*Note added in correcting the proof.*]
(2) Essentially the formulae of sections (35) and (36), page 73, had been given by DETLEFSEN (1914, p. 95). DETLEFSEN includes in *n* the first cross, so that his formulae are stated in slightly different terms. I regret that I overlooked DETLEFSEN's work, which contains much of great interest on the theoretical results of continued inbreeding.
(3) In the example under section (28), page 70, the value for *aa* should be 85/144 in place of 91/144.
(4) In table 1, series L, under "How formed," read "B_n F_{n-1} G_{n-1}."

each case the dominant factor. *In giving the constitution of an individual the juxtaposition of the letters will indicate the constitution of the gametes from which the individual was formed, and consequently at the same time the linkage,* if there is linkage. Thus the individual *ABab* is formed from the gametes *AB* and *ab,* and if there is linkage, this is between *A* and *B* on the one hand, between *a* and *b* on the other. The individual *AbaB* was formed from the gametes *Ab* and *aB,* and the linkage, if any, is between *A* and *b* on the one hand, *a* and *B* on the other.

(2) LINKAGE; DESIGNATION OF THE LINKAGE RATIO *r*

When two pairs of factors are dealt with, these may be independent or linked. In the former case any possible combination of the two pairs occurs in the gametes as frequently as any other. But when two factors are linked, the combinations found in the gametes which produced the given parents occur in the gametes produced by those parents more frequently than do other combinations. Thus, if the individual *ABab* was produced by union of the two gametes *AB* and *ab,* then when this individual forms gametes, there will be more gametes of the constitutions *AB* and *ab* than of the constitutions *Ab* and *aB*.

We shall designate the linkage ratio by the letter *r*. This number *r* indicates therefore the number of gametes showing the same combination of factors that occurred in the foregoing generation of gametes, in proportion to 1 showing other combinations. Thus, if in the case just cited, there are produced 3 gametes of the constitution *AB* (or *ab*) to 1 of *Ab* (or *aB*), the value of the linkage ratio *r* is 3. It is practically important to observe that for the working out of numerical proportions, "independence" of factors is merely a special case of linkage,—the particular case in which the value of the linkage ratio *r* is 1. Thus, if we derive general formulae for the results of linkage, these will include also the results when the factors are independent; in the latter case for numerical results it will merely be necessary to give to the letter *r* the value 1. As is well known, the value of *r*, the linkage ratio, may vary in different cases from 1 up to 80 or 100, or more.

In certain known cases, where linkage occurs, it is complete in one sex, the two factors involved acting in that sex like a single one. Thus, from the parent *ABab* there are produced in one sex but two sorts of gametes, *AB* and *ab,* in equal proportions, while the other sex gives *r AB* : 1 *Ab* : 1 *aB* : *r ab*. It is not certain that this completeness of the linkage in one sex holds for all organisms, so that we shall deal both

with this case, and the case in which linkage is the same in both sexes.

The relative frequency with which the different gametes are formed of course affects the frequency with which individuals (zygotes) with particular combinations of factors appear in the next generation. Our task is to discover general formulae for the proportions of the different classes of zygotes with respect to two characters, whatever the degree of linkage; formulae from which numerical results are obtainable when the proper values are substituted for r. The solution of this problem is quite independent of the question of the cause of linkage. It merely requires that there shall be in each case some fairly constant average ratio between the number of gametes which show the original combinations and those which show the new combinations; the work of many investigators has shown that this is the case.

When two pairs of factors are dealt with, whether linked or independent, it is not possible from a knowledge of the constitution of the zygotes with respect to each pair taken separately, to tell how the two pairs will be combined; the rules of combination must be worked out for themselves. This principle will receive illustration in the present paper (see section (21)).

(3) METHOD

With respect to two pairs of factors there are 4 diverse sorts of gametes, *AB, Ab, aB* and *ab*. The combinations of these 4 kinds of gametes give 10 diverse kinds of zygotes; these and their origin from the gametes are illustrated in table 6. Owing to this considerable number of diverse kinds of zygotes, direct formulae for the zygotes of a later generation in terms of those of an earlier generation become complex, unless we begin with parents of a single simple type. On this account it is, wherever possible, simpler to break the computation into two steps: (1) to obtain the proportions of the four different kinds of gametes derivable from the given zygotes; (2) from the gametic proportions thus reached, the proportions of the different sorts of zygotes for the next generation are obtained. We shall therefore present formulae for each of these steps, and the computations for any particular case will usually require the use of both these formulae, save in special cases where it is possible to develop single, more comprehensive, formulae.

This method of proceeding by two steps (first finding the gametes, then from these the zygotes) depends upon the principle that ***random mating of zygotes gives the same results as random mating of the***

gametes which they produce. The particular way in which the gametes have been united in the parental zygotes does not affect the results of random mating. This principle is easily demonstrated algebraically.

Where the mating is not at all at random, as in self-fertilization, the principle cannot be employed; we must devise formulae for the direct transformation of one generation of zygotes into a later one.

(4) TWO CLASSES OF FORMULAE; GENERAL AND SPECIAL

Two classes of formulae are obtainable:

General formulae for transforming generation n into generation n + 1. One class is of *general* application, so that whatever the constitution of the parental population, by means of the formulae the constitution of the population in later generations is obtainable. For example, the original population may be composed of diverse individuals in the proportions 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB*, and we may desire to know the constitution of the population in some later generation after breeding by random mating or assortative mating, or the like. Such general formulae can as a rule be given only for determining the constitution of the next following generation; the formulae can then be reapplied for determining the constitution of the next generation, and so on indefinitely. Thus such general formulae may be characterized as formulae for transforming generation *n* into generation *n* + 1.

Special formulae for parents ABab, etc. The second class consists of special formulae, for important particular cases, the main such case being that in which the original parents are all alike and are of the type *ABab* or *AbaB*. For such parents, which represent the case to which the formulae will most commonly be applied, it is possible, for some systems of breeding, to obtain formulae that will give directly the constitution of the population in any later generation, without working out the constitution in the intervening generations. For example, if the original progenitors are *ABab*, we may by a proper formula determine at once what will be the constitution of the population after seven successive random matings, or ten successive self-fertilizations, or the like.

(5) ORDER OF TREATMENT

We shall first set forth the different classes of zygotes and gametes with respect to two pairs of factors, and propose algebraic designations for the proportional numbers in which each occurs in any case.

We shall then take up the derivation of the general and special formulae for each system of breeding, dealing separately with the cases

in which linkage is the same in the formation of both sorts of gametes, and that in which linkage is complete in forming one of the sets of gametes. The formulae derived will be grouped in a series of numbered tables, which for convenience of reference will be placed all together at the end of the paper.

(6) CLASSES OF ZYGOTES WITH RESPECT TO TWO PAIRS OF FACTORS, AND THEIR DESIGNATIONS

With respect to two pairs of factors, and having regard to linkage, there are ten diverse types of zygotes, the origin of which is illustrated in table 6. Any or all of these ten types may be included, in various proportions, in any population. The proportional numbers of these various classes of zygotes in any generation will be designated by the letters *c* to *l*, with the significations shown in table 1 (page 141). In table 1 we classify as homozygotes those that are homozygotic with respect to both pairs of factors; as heterozygotes those heterozygotic with respect to both pairs of factors; as mixed those homozygotic with respect to one pair, heterozygotic with respect to the other. Any population may be represented by table 1, when proper values are given to the letters *c* to *l*.

In the later treatment the letters *c* to *l* will be used to designate in brief the proportions of the various types of zygotes to which the given letter is assigned in this table 1; thus, *g* will be understood to signify always the number of zygotes having the constitution *ABab*; *j* the number of *ABaB*, etc. In specific cases the values of *c* to *l* will be diverse. Thus in the population composed of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB*, the value of *c* is 3, $f = 1$, $h = 1$, $j = 4$, while the value of the other letters is 0.

(7) CLASSES OF GAMETES WITH RESPECT TO TWO PAIRS OF FACTORS, AND THEIR DESIGNATIONS

There are four classes of gametes with respect to two pairs of factors. We shall designate their (relative) numbers in any given case by the letters *p*, *q*, *s* and *t*, with the significations shown in table 2 (page 141).

As in the case of the zygotes, so here, the letter *p* will at times be used by itself to designate the number of gametes of the type *AB*, *q* the number of *Ab*, etc.

II. RANDOM MATING

We shall first obtain formulae for the proportional numbers of the different sorts of gametes produced by any population of zygotes (of

generation n); these will be the gametes for producing generation $n + 1$.

Next we shall get formulae for the zygotes (of generation $n + 1$) resulting from the random mating of this (or of any) set of gametes.

Third, we shall develop formulae by which the proportions of the *gametes* for the next following generation may be obtained when we know the proportions of the gametes for the foregoing generation,—so that the proportions of the zygotes may be omitted from consideration until the generation is reached for which the zygotic proportions are desired.

Finally we shall take up special formulae for particularly important cases, such as that in which the original parents are all *ABab* or *AbaB*.

DERIVATION OF THE PROPORTIONS OF THE DIFFERENT KINDS OF GAMETES PRODUCED BY ANY KNOWN SET OF ZYGOTES

Any population of zygotes may be represented in the way shown in table 1, by giving proper values to $c \ldots l$. Our present question is: What will be the relative numbers of the four different sorts of gametes produced by such a population? Or since the relative proportions of the four sorts of gametes are designated by the letters p, q, s and t (table 2), what we require is to derive the values of p, q, s and t in terms of c to l (of table 1).

In deriving the gametes from the zygotes, it is to be remembered that the original gametic union that produced the zygotes of table 1 (and hence the linkage), is indicated by the juxtaposition of the letters, and that the linkage ratio is r.

(8) LINKAGE RATIO $= r$

Taking first one of the heterozygotes, as *ABab*, the gametes are r *AB* : 1 *Ab* : 1 *aB* : r *ab*. In order to realize these proportions it is evidently necessary that each such zygote should produce $2r + 2$ gametes. To keep the proportions correct throughout, each gamete of table 1, whatever its constitution, must be considered to produce $2r + 2$ gametes, although from a homozygote these will all be alike, and from a mixed zygote there will be but two sorts, in equal numbers. We shall therefore find that the zygotes of table 1 give the gametes shown in the first column of table 3.

Having obtained table 3, we collect from the column "linkage $= r$" the various values for each of the four kinds of gametes *AB*, *Ab*, *aB* and *ab*. As in table 2, the total values for the different kinds are to be designated p, q, s and t, respectively. By collecting we obtain table 4.

(9) LINKAGE COMPLETE

In the case that the linkage is complete in forming one of the sets of gametes, the proportions of the gametes of that set will not be those in table 4. Where linkage is complete, each parent zygote produces but two kinds of gametes in equal number,—these being the same two kinds by which this parent was formed. Thus the individual *ABab* produces gametes *AB* and *ab* in equal numbers; the individual *AbaB* produces *Ab* and *aB*, etc. To get the correct proportions throughout we require to assume only that each zygote produces two gametes. The results are given in the second column of table 3. Collecting the values for the four sorts of gametes, and calling their proportions, when linkage is complete, by the capital letters *P*, *Q*, *S* and *T*, in place of the corresponding small letters, we obtain table 5.

(10) DETERMINATION OF THE PROPORTIONS OF THE DIFFERENT CLASSES OF ZYGOTES PRODUCED BY THE RANDOM MATING OF ANY SET OF GAMETES

The population at the beginning is that shown in table 1 (which of course represents any population whatever, if the correct values are given to the letters *c* to *l*). The proportions of the gametes (that is, the values of *p*, *q*, *s* and *t*) are determined by table 4.

Having thus obtained the values of *p*, *q*, *s* and *t*, we must next observe the zygotes produced by the random mating of the four sets of gametes, *p* . *AB*, *q* . *Ab*, *s* . *aB* and *t* . *ab*. The mating and results are represented in table 6.

It will be observed that of the resulting zygotes (table 6), the four forming the diagonal from the left upper corner to the right lower corner are homozygotes; the four forming the other diagonal are heterozygotes, and the other eight are mixed. The zygotes resulting from the first random mating ($n = 1$) are therefore those shown in table 7.

Table 7 is the fundamental general table for determining the zygotic proportions resulting from the random mating of any given set of gametes. It will be employed in working out the results of selection and of assortative mating, as well as of random mating.

Example. Tables 4 and 7 furnish the formulae for the two steps necessary to obtain the proportional numbers of the different classes of individuals (zygotes) in the generation $n + 1$, when we know those in generation n,—the mating being at random, and the linkage being the same for both sets of gametes.

For example, suppose that the original population consists of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB;* that the linkage ratio *r* is 2, and that breeding is by random mating. What various types of individuals will be present in the next generation, and in what proportions?

Here evidently (referring to table 1),—

$$c = 3,\quad f = 1,\quad h = 1,\quad j = 4$$

while *d, e, g, i, k* and *l* are 0. Therefore the gametes produced will be, by table 4 (since $r + 1 = 3$):

$$\begin{aligned} p &= 3.\ (6 + 4) + 1 = 31 \\ q &= 2.1 \qquad\quad = 2 \\ s &= 3.4 + 2.1 \qquad = 14 \\ t &= 3.2 + 1 \qquad\quad = 7 \\ p + q + s + t &\qquad = 54 \end{aligned}$$

The gametes will therefore be in the proportions 31 *AB* : 2 *Ab* : 14 *aB* : 7 *ab*.

Then the zygotes of the next generation ($n + 1$) will be, by table 7, the following:

ABAB	$= 31^2 = 961$	*AbaB*	$= 2.2.14 = 56$
AbAb	$= 2^2 = 4$	*ABAb*	$= 2.31.2 = 124$
ABaB	$= 14^2 = 196$	*ABaB*	$= 2.31.14 = 868$
abab	$= 7^2 = 49$	*abAb*	$= 2.2.7 = 28$
ABab	$= 2.31.7 = 434$	*abaB*	$= 2.14.7 = 196$

By now substituting these values for *c* to *l* in table 1, and using anew tables 4 and 7, we may find the zygotic proportions for the third generation, and so on indefinitely. If desired the values for *c* to *l* may be reduced to decimal fractions in each case, giving all later proportions in decimals.

(11) Determination of the proportions of the different classes of zygotes produced where one set of gametes formed with linkage (*r*) (table 4) mates with another set with complete linkage (table 5)

This represents what appears to be the usual condition, where the gametes from one sex (eggs or sperm) are produced with linkage *r*, the other set with complete linkage.

In this case, as usual, the population at the beginning is that in table 1.

We determine by table 4 the values for p, q, s and t, and by table 5 the values for P, Q, S and T.

Now to obtain the zygotic proportions in the next generation, in table 6 we substitute in one of the columns of gametes the values P, Q, S and T for p, q, s and t; then we multiply as before to obtain the 16 lots of zygotes. Having performed this operation and classified the results in the same way as was done for table 7, we obtain for the zygotic proportions the table 8.

Example. To transform the zygotes of generation n into those of generation $n + 1$, when linkage is complete in one set of the gametes, we therefore use successively the formulae of tables 4, 5 and 8. Suppose that we take the same example given in section (10), page 106, but assume that linkage is complete in one set of gametes.

Then by tables 4 and 5 the two sets of gametes are:

$p = 31$	$P = 10$
$q = 2$	$Q = 1$
$s = 14$	$S = 5$
$t = 7$	$T = 2$

And by table 8 the individuals (zygotes) of the next generation $(n + 1)$ are:

$ABAB = 310$	$AbaB = 24$
$AbAb = 2$	$ABAb = 51$
$aBaB = 70$	$ABaB = 295$
$abab = 14$	$abAb = 11$
$ABab = 132$	$abaB = 63$

By substituting these values for c to l in table 1, we may determine the proportions of the different types of individuals in the next later generation, and so on. We may of course, if we prefer, reduce all the proportions to decimal fractions, and employ these decimals in working out results for later generations.

DERIVATION OF THE GAMETES PRODUCED BY THE NEXT GENERATION OF ZYGOTES (GENERATION $n + 1$), WHEN THE GAMETES PRODUCED BY THE FOREGOING GENERATION (GENERATION n) ARE KNOWN

If it be desired to determine the zygotic constitution of the population in some later generation (as for example the fifth), it saves much labor to deal for the intervening generations with the gametes alone. That is, by formulae to be set forth, we determine directly from the proportions of the gametes produced by generation 1 the proportions

of the gametes produced by generation 2; thence the gametic proportions from generation 3; thence those from generation 4, thence from 5. Only for this final generation do we determine the zygotic proportions.

Our problem is therefore to obtain p_{n+1}, q_{n+1}, s_{n+1} and t_{n+1} from p_n, q_n, s_n and t_n.

(12) *Linkage the same in both sets of gametes*

To derive our formulae, we first obtain the gametes from the original parents (generation n) by table 4; then from these gametes we derive the zygotes (generation $n + 1$) by table 7. From these zygotes, by the method of section (8) and table 3, we find that the gametes produced are the following:

Zygotes of $n + 1$		*Gametes from* $n + 1$
$p^2.ABAB$	=	$p^2.(2r + 2)\ AB$
$q^2.AbAb$	=	$q^2.(2r + 2)\ Ab$
$s^2.aBaB$	=	$s^2.(2r + 2)\ aB$
$t^2.abab$	=	$t^2.(2r + 2)\ ab$

$$2pt.ABab = 2pt.r.AB + 2pt.Ab + 2pt.aB + 2pt.r.ab$$
$$2qs.AbaB = 2qs.r.Ab + 2qs.AB + 2qs.ab + 2ps.r.aB$$

$$2pq.ABAb = 2pq.(r+1)\ AB + 2pq.(r+1)\ Ab$$
$$2ps.ABaB = 2ps.(r+1)\ AB + 2ps.(r+1)\ aB$$
$$2qt.abAb = 2qt.(r+1)\ ab + 2qt.(r+1)\ Ab$$
$$2st.abaB = 2st.(r+1)\ ab + 2st.(r+1)\ aB$$

Collecting the values for the gametes AB, Ab, aB, and ab, (from $n + 1$), and removing from each the factor 2, we obtain the formulae given in table 9.

By the continued use of these formulae we may find the proportions of the different gametes produced by any later generation of random mating, without troubling to find the zygotic constitution in any generation save the final one in which we are primarily interested. At any time the zygotic constitution is found by the formulae of table 7.

(13) *Independent factors*

If the factors are independent ($r = 1$), the gametic formulae of table 9 may be simplified through the substitution of 1 for r, giving table 10.

Example. In the example given in section (10), the following values were found for p, q, s and t for the first random mating:

$$p = 31 \qquad q = 2 \qquad s = 14 \qquad t = 7$$

Then by the formulae of the table 9 the values of p, q, s and t for the second random mating will be (when $r = 2$):

$$\begin{aligned} p &= 3.31.47 + 2.31.7 + 2.14 = 4833 \\ q &= 3.2.40 + 2.2.14 + 31.7 = 513 \\ s &= 3.14.52 + 2.2.14 + 31.7 = 2457 \\ t &= 3.7.23 + 2.31.7 + 2.14 = 945 \\ p + q + s + t &= 3.54^2 = 8748 \end{aligned}$$

Now by the formulae of table 7, we may if we desire, obtain from these results the relative numbers of the different kinds of zygotes resulting from the second random mating.

Or we can by a repeated use of the formulae of the present section obtain the gametic constitution for the third, fourth and later generations; finding in addition the zygotic constitution for any desired generation.

(14) *Linkage complete in one sex, r in the other*

In this case we derive two sets of gametes from the original parents, by means of tables 4 and 5, and these give for generation $n + 1$, the zygotes of table 8. From these zygotes of table 8, we must find two sets of gametes, one with linkage r (by the method illustrated in section (8)), the other with complete linkage (by the method illustrated in section (9)). We must assume that both sexes are represented in each kind of zygote of table 8, so that we must form a first set of gametes from all the kinds of zygotes of table 8 by the method of section (8), then a second set from all by the method of section (9). Performing these operations and collecting the results, we obtain table 11.

In comparing the gametes of set 1 with those of set 2 (in table 11) certain constant relations between the two sets become evident. These are shown in table 12. These relations are of consequence for certain problems, particularly in selection and assortative mating; they are also useful in checking up the correctness of computations.

Example. We will take the example employed in section (10), but now assuming that linkage is complete in one sex. The parent zygotes were $3\,ABAB + 1\,abab + 1\,AbaB + 4\,ABaB$; and $r = 2$.

As shown in section (10), before the first random mating the gametes of the first set, with linkage r, are:

$$p = 31 \qquad q = 2 \qquad s = 14 \qquad t = 7$$

According to section (11), further, the gametes of the second set, with complete linkage, are:

$$P = 10 \qquad Q = 1 \qquad S = 5 \qquad T = 2$$

The zygotes resulting from the first random mating are therefore, by table 8:

ABAB	$= 31.10 = 310$	*AbaB*	$= 1.14 + 2.5 = 24$
AbAb	$= 2.1 = 2$	*ABAb*	$= 10.2 + 31.1 = 51$
aBaB	$= 14.5 = 70$	*ABaB*	$= 10.14 + 31.5 = 295$
abab	$= 7.2 = 14$	*abAb*	$= 1.7 + 2.2 = 11$
ABab	$= 10.7 + 31.2 = 132$	*abaB*	$= 5.7 + 14.2 = 63$

The gametes for the second random mating ($n = 2$) are obtained from the values of p_1, q_1, etc., given above, by the formulae of table 11, giving the following:

Set 1: Linkage $r = 2$, in both sexes:

$$p_2 = 3.31.16 + 3.10.47 + 2.(70 + 62) + 14 + 10 = 3186$$
$$q_2 = 3.2.13 + 3.1.40 + 2.(14 + 10) + 70 + 62 = 378$$
$$s_2 = 3.14.17 + 3.5.52 + 2.(14 + 10) + 70 + 62 = 1674$$
$$t_2 = 3.7.8 + 3.2.23 + 2.(70 + 62) + 14 + 10 = 594$$
$$p + q + s + t = 5832$$

Set 2: Linkage complete in one sex:

$$P_2 = 10.54 + 31.18 = 1098$$
$$Q_2 = 1.54 + 2.18 = 90$$
$$S_2 = 5.54 + 14.18 = 522$$
$$T_2 = 2.54 + 7.18 = 234$$
$$P + Q + S + T = 1944$$

It will be observed that the sum $(p + q + s + t)$ is just 3 times the sum of $(P + Q + S + T)$, 3 being the value of $(r + 1)$.

Now by table 8 we may if we desire find the proportions of the different zygotes resulting from the second random mating; or we may omit this, and find directly the two sets of gametes for the third random mating; and so on.

RANDOM MATING: SPECIAL FORMULAE

(15) *Parents all ABab*

For the specially important case in which the parents are a first cross between *ABAB* and *abab*, (so that they are themselves *ABab*), we may obtain a general formula which shall give us directly the proportions of gametes (and indirectly of zygotes) for producing any generation *n*, without working out the proportions for intervening generations. For this the following points must be noticed:

Evidently the number of gametes *AB* is the same as the number of *ab;* while the number of *Ab* is the same as of *aB*, and this equivalence will be found to hold throughout random mating. We have therefore, so far as the gametes go, but two unknown quantities to deal with in place of four. In tables 2 and 5, therefore, we can put:

$$p = t \qquad P = T \qquad q = s \qquad Q = S$$

We require therefore but to find p, P, q and Q; these will give us the others.

Now, if at the beginning the parents are all *ABab*, and the linkage ratio is r, then evidently the gametes from these parents are r *AB* : 1 *Ab* : 1 *aB* : r *ab*, so that for producing generation 1 the gametes are:

$$p = r \qquad q = 1 \qquad p + q = r + 1 \qquad p - q = r - 1$$

In the sex (if there is such) in which the linkage is complete, the gametes formed by *ABab* are evidently simply *AB* and *ab* in equal numbers, so that (for producing generation 1):

$$P = 1 \qquad Q = 0 \qquad P + Q = 1 \qquad P - Q = 1$$

(16) Linkage r in both sets of gametes, parents all *ABab*

Now, if we take first the case in which linkage is r in both sexes, we may by table 9 from the above gametic proportions for producing generation 1 determine the gametic proportions for producing generation 2. We shall find these to be as follows:

$$p_2 = 2r^3 + 3r^2 + 2r + 1 = (r + 1)(2r^2 + r + 1)$$
$$q_2 = \quad 3r^2 + 4r + 1 = (r + 1)(3r + 1)$$

Since it is the relative proportions that we desire, we can take out the common factor $(r + 1)$, and we have:

$$p_2 = 2r^2 + r + 1$$
$$q_2 = \quad 3r + 1$$
$$p_2 + q_2 = 2r^2 + 4r + 2 = 2(r + 1)^2$$
$$p_2 - q_2 = 2r^2 - 2r = 2(r^2 - r)$$

If we continue in this way, finding successively the values of p_3, p_4, p_5, q_3, q_4, q_5, etc., certain general relations manifest themselves, particularly with regard to the sums of p and q, and their differences. It turns out that for producing any generation n

$$p_n + q_n = 2(r+1)^n$$
$$p_n - q_n = 2(r^n - r^{n-1})$$

Solving these two equations for the values of p_n and q_n (and omitting from the result the common factor, 2), we obtain the formulae of table 13.

Having determined the values of p_n, q_n, s_n and t_n by table 13, the proportions of the different classes of individuals (zygotes) in generation n is obtained from table 7.

(17) If there is no linkage ($r = 1$) and the parents are all *ABab* the population will be found to remain constant, in the following proportions:

The four sorts of homozygotes, each = 1
The two sorts of heterozygotes, each = 2
The four sorts of mixed, each = 2

Example. Parents all *ABab*, linkage ratio $r = 3$. What will be the constitution of the population (zygotes) after 4 random matings? By table 13:

$p_4\ (= t_4) = 4^4 + 3^4 - 3^3 = 310$
$q_4\ (= s_4) = 4^4 - 3^4 + 3^3 = 202$
$p^2\ (= t^2) = 96{,}100$
$q^2\ (= s^2) = 40{,}804$
$2pq\ (= 2st) = 125{,}240$
Total zygotes $= (620 + 404)^2 = 1024^2 = 1{,}048{,}576.$

From which it is evident that by the zygotic formulae of table 7 the proportions of the different sorts of zygotes are:

$$ABAB = \frac{96{,}100}{1{,}048{,}576} = .0916$$
$abab = .0916$
$AbAb = .0389$
$aBaB = .0389$
Total homozygotes = .2611
$ABab = .1833$
$AbaB = .0778$
Total heterozygotes = .2611
Each of 4 sorts of mixed = .1194
Total mixed = .4778

(18) Parents all *ABab;* linkage r in one set of gametes, complete in the other

Here, as in section (15), the number of gametes AB is equal to that of ab, while the number of Ab is equal to that of aB, so that:

$$p = t \qquad q = s \qquad P = T \qquad Q = S$$

Also, as we saw in (15), for the first mating ($n = 1$):

$$p = r \qquad q = 1 \qquad P = 1 \qquad Q = 0$$

$$p + q = r + 1; \quad p - q = r - 1; \quad P + Q = 1; \quad P - Q = 1.$$

Now by the use of table 11, we obtain the corresponding values of p, q, P and Q for producing generation 2. We find thus that:

$$\begin{aligned} p_2 &= 2r^2 + 2r + 1 & P_2 &= 2r + 1 \\ q_2 &= \quad 2r + 1 & Q_2 &= \quad 1 \\ p_2 + q_2 &= 2(r + 1)^2 & P_2 + Q_2 &= 2(r + 1) \\ p_2 - q_2 &= 2r^2 & P_2 - Q_2 &= 2r \end{aligned}$$

Now if by continued use of table 11, we find the corresponding values for successive generations, we discover that for any number n of generations the gametes which mate to form that generation show the following relations:

$$\begin{aligned} p_n + q_n &= 2^{n-1}(r + 1)^n \\ p_n - q_n &= 2r^2\ (2r + 1)^{n-2} \\ P_n + Q_n &= 2^{n-1}(r + 1)^{n-1} \\ P_n - Q_n &= 2r\ (2r + 1)^{n-2} \end{aligned}$$

Solving these equations for the values of p, q, P and Q, we obtain the formulae of table 14.

Having determined thus the proportions of the gametes, the constitution of generation n in zygotes is obtained by the use of table 8.

Example:—Parents *ABab;* linkage ratio $r = 3$; four generations of random mating ($n = 4$). What is the constitution of the population? By table 14, the gametic proportions preliminary to generation 4 will be:

$$\begin{aligned} p_4 &= 2^2 \cdot 4^4 + 9 \cdot 7^2 = 1465 \\ q_4 &= 2^2 \cdot 4^4 - 9 \cdot 7^2 = 583 \\ p_4 + q_4 &= 2048 \\ P_4 &= 2^2 \cdot 4^3 + 3 \cdot 7^2 = 403 \\ Q_4 &= 2^2 \cdot 4^3 - 3 \cdot 7^2 = 109 \\ P_4 + Q_4 &= 512 \end{aligned}$$

To obtain the zygotes resulting from the mating of these gametes it is well to note the following:

$$Pp = 590{,}395$$
$$Qq = 63{,}547$$
$$Pq = 234{,}949$$
$$pQ = 159{,}685$$
$$Pp + Qq + Pq + pQ = 1{,}048{,}304$$

Then by table 8 (remembering that $p = t$, $q = s$, $P = T$ and $Q = S$), we find that the total number of zygotes $(P + Q + S + T)$ $(p + q + s + t)$ is 4,194,304. Working out, by table 8, the proportions for each of the classes of zygotes, and dividing each by 4,194,304 in order to reduce them to decimals, we find that the population in the fourth generation is:

Homozygotes, *ABAB* and *abab*, each	.141
AbAb and *aBaB*, each	.015
Total	.312
Heterozygotes, *ABab*	.282
AbaB	.030
Total	.312
Mixed, four sorts, each	.094
Total mixed	.376

(19) *Parents AbaB; linkage r in both sets of gametes*

In this case simply interchange the values of p and q in table 13 (of course therefore also the values of t and s), then obtain the zygotic proportions by table 7.

(20) *Parents AbaB; linkage r in one set of gametes, complete in the other*

In this case simply interchange the values of p and q; also of P and Q, in table 14 (of course therefore also the values of t and s, as well as of T and S); then obtain the zygotic constitution by table 8.

(21) *Original parents ABAB and abab in equal numbers, random mating*

In this case if there is linkage the proportions of gametes and zygotes for any generation must be worked out by the general formulae for random mating, given in sections (8) to (14).

When there is no linkage ($r = 1$) it is instructive to compare this

case with that in which the parents are all *ABab* (and there is no linkage). If we examine the results with respect to single pairs of characters taken separately, we find them to be identical for the two cases. That is, when the parent population is either *ABab*, or is *ABAB* + *abab*, random mating gives for all later generations with respect to one pair of characters the uniform constitution ¼ *AA* + ½ *Aa* + ¼ *aa*; with respect to the other the constitution ¼ *BB* + ½ *Bb* + ¼ *bb*. But when we consider the two pairs together, we find that the two cases give diverse results; the two pairs of characters are combined diversely in the two cases. This is therefore an example of the fact, mentioned in section (2), that we cannot from a knowledge of the constitution with respect to two pairs of characters taken separately determine what will be the constitution with respect to combinations of the two pairs. In the case of the population derived from the random mating of *ABab*, the proportion of any combination of the two pairs is merely the product of the proportions for the two component pairs taken separately, thus the proportion that are *AABb* is ¼ × ½ = ⅛, etc. But when the original parents are *ABAB* + *abab*, this rule does not hold. The gametes from such parents are in any generation n the following:

$$p_n = t_n = 2^{n-1} + 1$$
$$q_n = s_n = 2^{n-1} - 1$$

The zygotic proportions are then obtainable by table 7. It will be found that these zygotic proportions change from generation to generation, although for each pair of characters taken by itself the proportions are constant. The zygotic proportions in successive generations are:

Random matings	1	2	3	n
ABAB and *abab*, each	4	9	25	D^2_n
AbAb and *aBaB*, each	0	1	9	C^2_{n-1}
ABab	8	18	50	$2D^2_n$
AbaB	0	2	18	$2C^2_{n-1}$
Mixed, 4 sorts, each	0	6	30	$2D_nC_{n-1}$

For the n'th generation the proportions are above given in terms of the series of table 1 in my earlier paper (JENNINGS 1916); thus the value for *ABAB* and *abab* is the square of the n'th term of series D of that paper; the value for *AbaB* is twice the square of the $(n-1)$th term of series C of that paper, etc.

III. Selection with relation to a single character

Suppose that in breeding, selection is exercised with respect to a single character forming one of a pair; for example suppose that of the pair *A* and *a*, individuals showing the character *A* are always selected for further propagation. In our previous contribution (Jennings 1916) we have dealt with the results on the constitution of the population with respect to this pair on which selection is based. But what will be the effect on the constitution with respect to another pair of factors, *B* and *b*, which is linked with the pair on which selection is based? That is, in a population composed of individuals having *A*, *a*, *B* and *b* in the various possible combinations, what will be the resulting constitution due to selecting for the character *A* for a given number *n* of generations?

We shall take up first the case in which the selected character is dominant, next that in which it is recessive. We may proceed upon the same general plan employed for random mating, employing primarily the proportions of gametes in the successive generations as the bases for our work, and deriving the proportions of zygotes secondarily from those for the gametes that produce them.

Selection of dominants with respect to one of the pairs of characters; general formulae

(22) *Gametes produced when there is selection of dominants with respect to one pair*

If we have such a population as is shown in table 1, and breed only from those that are dominants with respect to the pair *A* and *a*, this is equivalent to omitting all the zygotes that do not contain *A;* that is, it omits *e*, *f* and *l* of table 1. The gametes produced when there is such selection of dominants are therefore in the proportions shown in table 15 (compare with tables 4 and 5).

(23) *Proportions of the different classes of zygotes produced in the next generation (n + 1), when the breeding is by selection for dominant A*

The selection has taken place in the production of the gametes (table 15). These gametes now simply mate at random, so that we can employ directly the tables 7 and 8, for random mating. Therefore when there is selection for dominant *A*, the procedure for finding the proportions of the population in the next generation is as follows:

First give the proper values to the letters *c* to *l*, in table 1, and to *r*.

If linkage is the same ($=r$) in both sets of gametes, employ first the formulae of table 15, (set 1); then those of table 7; this gives the different classes of individuals in the next generation $n+1$.

If linkage is complete in one set of gametes, employ first table 15 (both sets), then table 8; thus obtaining the proportions of the different classes of individuals in the next generation $(n+1)$.

If it be desired to find the zygotic proportions only for some later generation (as for example the seventh), it is not necessary to find the zygotic proportions for the intervening generations, but one works for these intervening generations with the gametes alone, according to the methods of the following sections (24) and (25).

(24) *Derivation of the gametes produced by the next generation (n+1) of zygotes, when the gametes produced by the preceding generation n are known, (breeding by selection of dominant A)*

If we desire to obtain the zygotic proportions only for some later generation, we may work for the intervening generations only with the gametes, by methods analogous to those set forth for random mating

Linkage the same ($=r$) in both sexes. We use the method set forth in sections (12), (13) and (14).

in section (12), but exclude from gamete formation the zygotes *aBaB*, *abab*, and *abaB* (since these do not contain *A*). We thus obtain the formulae given in table 16.

Of course the zygotic proportions for generation $n+1$ may now if desired be found from the zygotic formulae of table 7. Or by repeated use of these formulae of table 16 we may find the gametic proportions for any later generation, then by table 7 find the zygotic proportions for that generation.

(25) *Linkage complete in one set, r in the other*

Derivation of the gametes that produce the succeeding generation $(n+1)$, from those that produce the preceding generation (n)

We use the methods set forth in (14), but exclude from gamete formation the zygotes *aBaB*, *abab* and *abaB* (since these do not contain *A*). The formulae we require are indeed obtained directly from those of table 11, by omitting in all cases the factors *Ss*, *Tt*, *St* and *sT*. The results are given in table 17.

By the repeated use of the formulae of this table 17, we may find the gametic proportions for any later generation; then by table 8 find

the zygotic proportions for that generation. See the example in section (27).

No formula has been found obtainable for determining the proportions in any given later generation *n*, without working out the values for the intervening generations. Even when the original parents are *ABab* or *AbaB*, the general methods (22) to (25) must be employed. The most important case, in which the original parents are *ABab*, will be found worked out illustratively in section (27).

(26) SELECTION OF DOMINANTS WITH RESPECT TO ONE OF THE PAIRS OF CHARACTERS; SPECIAL FORMULAE FOR THE EFFECT ON THE OTHER PAIR

Possibly the most interesting question in selection with reference to one pair of characters is its effect on another pair of characters, linked with the first pair. We shall take this up here, giving formulae for both the single factor-pairs taken separately.

Proportions of the single factor-pairs taken separately, when there is selection of dominant *A:* From the formulae of table 15, or of tables 16 and 17, taken in connection with those of tables 7 and 8, as set forth in sections (22) to (25), we may readily obtain for the desired generation the proportions of the population with relation to the members of either pair of factors taken separately; that is, with relation to *A* and *a;* or to *B* and *b*. After obtaining for the next generation the gametic proportions of table 16 (if linkage is the same in both sets); or those of table 17 (if linkage is complete in one of the sets of gametes), we observe that the gametic proportions for *A* and *a*, and for *B* and *b*, are those given in table 18.

The zygotic proportions in the next generation $(n + 1)$ are then, with relation to the single factor-pairs taken separately, those given in table 19.

The same proportions for each pair separately would be obtained by deriving the zygotic proportions for the two pairs together according to (24) and (25), then tabulating the constitution with reference to the factors taken separately.

The formulae given in table 19 for *AA*, *Aa* and *aa* give the same results as are given in sections (19) to (24) of my earlier paper (JENNINGS 1916), in which a single pair of factors was considered by itself. The linkage of course has no effect on the proportions of the pair with reference to which selection is made.

With relation to *BB*, *Bb* and *bb*, the proportions depend on the amount of linkage; the formulae of the present section enable us to determine precisely how selection with reference to one character (*A*) affects the proportions with respect to another character linked with it (*B* and *b*). If there is no linkage ($r = 1$), the formulae given in table 19 for *BB*, *Bb* and *bb* give the same results as for those of random mating (sections (1) to (12) in my earlier paper); that is, selection with reference to *A* and *a* is random mating with reference to *B* and *b*, if the two pairs are not linked.

All these matters are illustrated in the concrete example given in the following sections (27) and (28).

(27) Illustrative example of the results of selecting dominants; parents all *ABab*

To illustrate the use of the formulae for selection of dominants, we will take the most important typical case, in which the parents at the beginning are the dihybrid *ABab*. We will determine the results for several generations of selecting for propagation only those having the dominant factor *A*. We shall compare the results when there is linkage and when there is none; also the results when linkage is alike in both sexes, and those when linkage is complete in one sex. To keep the numbers relatively small we shall assume the linkage to be 2.

As the original parents (*ABab*) all contain *A*, none are excluded in the first mating. When there is no linkage the gametes are evidently 1 *AB* : 1 *Ab* : 1 *aB* : 1 *ab*. When the linkage is 2, the gametes are 2 *AB* : 1 *Ab* : 1 *aB* : 2 *ab*.

No linkage ($r = 1$). In this case for the first mating, as we have seen, $p_1 = 1$, $q_1 = 1$, $s_1 = 1$, $t_1 = 1$. We now find the proportions for the succeeding generations, by the formulae of table 16. For the next generation ($n = 2$) they are evidently as follows (since $r + 1 = 2$).

$$\begin{aligned} p_2 &= 2.1.3 + 1.1 + 1 = 8\ (=2) \\ q_2 &= 2.1.3 + 1.1 + 1 = 8\ (=2) \\ s_2 &= 2.1 \quad + 1 \quad + 1 = 4\ (=1) \\ t_2 &= 2.1 \quad + 1 \quad + 1 = 4\ (=1) \end{aligned}$$

As it is only the proportional numbers that we desire, we may divide through by 4, giving the numbers in the last column.

Repeating our use of the formulae of table 16, we find that when

there is no linkage the gametic proportions for the first four generations are:

n =	1	2	3	4
p =	1	2	3	4
q =	1	2	3	4
s =	1	1	1	1
t =	1	1	1	1
	4	6	8	10

In general, it appears that for any generation n, p and q are each equal to n, while s and t are each 1.

Linkage 2, alike in both sexes ($r = 2$).

For generation 1, as we have seen, $p = 2$; $q = 1$; $s = 1$; $t = 2$. Applying now the formulae of table 16 and noting that $r + 1 = 3$, the proportions for generation 2 are found to be the following:

$$p_2 = 3.2.4 + 2.4 + 1 = 33 = 11$$
$$q_2 = 3.1.5 + 2.1 + 4 = 21 = 7$$
$$s_2 = 3.2 + 2.1 + 4 = 12 = 4$$
$$t_2 = 3.2 + 2.4 + 1 = 15 = 5$$

(We reduce to lowest integral terms by dividing all the proportions by 3.)

In the third generation, by renewed application of table 16, we find the proportions to be:

$$p_3 = 3.11.22 + 2.55 + 28 = 864 = 32$$
$$q_3 = 3.7.23 + 2.28 + 55 = 594 = 22$$
$$s_3 = 3.44 + 2.28 + 55 = 243 = 9$$
$$t_3 = 3.35 + 2.55 + 28 = 243 = 9$$

(We divide through by 27 to reduce to lowest terms.)

Thus when r is 2 in both sexes, the gametic proportions for the first four generations are:

n =	1	2	3	4
p =	2	11	32	379
q =	1	7	22	269
s =	1	4	9	86
t =	2	5	9	76
	6	27	72	810

Linkage complete in one sex; r = 2. In the sex in which the linkage is *r*, the parents *ABab* of course produce gametes in the proportions 2 *AB* : 1 *Ab* : 1 *aB* : 2 *ab;* these form the gametes of set 1. In the sex in which linkage is complete, the gametes formed are evidently 1 *AB* : 0 *Ab* : 0 *aB* : 1 *ab* (set 2). Using the letters *p*, *q*, *s* and *t* for the set 1 and *P*, *Q*, *S* and *T* for set 2, the gametes for the first generation ($n = 1$) are therefore:

Set 1	*Set 2*
$p = 2$	$P = 1$
$q = 1$	$Q = 0$
$s = 1$	$S = 0$
$t = 2$	$T = 1$

To obtain the gametic proportions in preparation for the next generation, we begin with the values just given, and employ the formulae of table 17. We thus find that for $n = 2$:

Set 1	*Set 2*
$p_2 = 3.2.1 + 3.1.4 + 2.4 + 0 + 0 = 26$	$P_2 = 1.6 + 2.2 = 10$
$q_2 = 3.1.2 + 3.0.5 + 2.0 + 2 + 2 = 10$	$Q_2 = 1.2 = 2$
$s_2 = 3.1 + 2.0 + 2 + 2 = 7$	$S_2 = 1.1 = 1$
$t_2 = 3.1 + 2.4 + 0 + 0 = 11$	$T_2 = 1.3 + 2.1 = 5$
54	18

Repeating the use of the formulae of table 17, but now beginning with the values for $n = 2$, and so on, we find that for the first four generations the gametic proportions are as follows (under each value of *n* is given in the first set the value of *p*, *q*, etc., in the second the value of *P*, *Q*, etc.):

n	1		2		3		4	
	Set 1	Set 2	Set 1	Set 2	Set 1	Set 2	Set 1	Set 2
p and *P* (= *AB*) =	2	1	26	10	117	42	310	108
q and *Q* (= *Ab*) =	1	0	10	2	45	12	122	36
s and *S* (= *aB*) =	1	0	7	1	24	5	53	13
t and *T* (= *ab*) =	2	1	11	5	30	13	55	23
Totals	6	2	54	18	216	72	540	180

Having now obtained the gametic proportions for each of the three diverse cases, it is a simple matter to compute for any generation the

proportions of the ten different sorts of zygotes. For the cases where the linkage relations are the same in both sexes we use the formulae of table 7; for the case where linkage is complete in one sex we employ the formulae of table 8. The results for the four generations are given in table 20. In each generation the results are given for the three diverse linkage relations; where r is given as 1 there is of course no linkage; where $r = 2$ the linkage ratio is 2 to 1 in both sexes; the third case, where the linkage is 2 to 1 in one sex and complete in the other, is indicated by putting $r = 2+$.

The results for each case are given twice; first as whole numbers, as they will be obtained from the formulae; then as decimal fractions, for comparison with the other cases. For example, in the first place of the first column we find $1 = .0625$. This means that out of the total 16 zygotes, one will be *ABAB*, and that this is equal to .0625 of the total.

(28) *The proportions for single factor-pairs taken separately; example:* In our example (27) we select entirely with reference to the pair *A* and *a*. The most interesting question doubtless is: What effect has this on the proportions of the various combinations of *B* and *b*, when the two pairs are linked?

This question may be answered from the formulae of table 19, employing the gametic proportions already given in table 20. We give the results for both the pairs, *A* and *a*, and *B* and *b*.

From table 19, the values are in the first generation:

When there is no linkage ($r = 1$):

$AA = 4$	$Aa = 8$	$aa = 4$
$BB = 4$	$Bb = 8$	$bb = 4$

When $r = 2$:

$AA = 9$	$Aa = 18$	$aa = 9$
$BB = 9$	$Bb = 18$	$aa = 9$

When $r = 2+$ (linkage complete in one sex):

$AA = 1$	$Aa = 2$	$aa = 1$
$BB = 1$	$Bb = 2$	$bb = 1$

Thus for this first generation all values of r give the same result for each of the combinations.

In later generations the results differ for the different values of r. Table 21 gives the proportions of the different combinations for the first four generations.

As table 21 shows, when there is linkage there is a steady increase in the proportion of *BB* over *bb*, as also of *BB* over *Bb*, as a result of selection for the character *A*.

SELECTION OF RECESSIVES

Only individuals *not* containing the factor *A* are selected for propagation. That is, selection is of individuals *aa* only.

We may deal at the same time with the two cases (1) where linkage is the same in both sexes, and (2) where linkage is complete in one sex, for the two give here the same results.

(29) *Gametes produced when there is selection of recessives with respect to one pair of factors*

Suppose that of the zygotes of table 1, only those that are recessive with respect to the pair *A* and *a* are bred, that is, only those that contain *aa*. In this case all zygotes are omitted except *e*, *f* and *l*. These give only gametes *aB* and *ab*, so that for the gametes we have only the proportions *s* and *t* to deal with. If we determine the gametic proportions in accordance with the principles in section (22), we find that

$$s = (r+1)(2e+1)$$
$$t = (r+1)(2f+1)$$

But as it is only the relative proportions that are important, we may divide both these by $(r+1)$, giving table 22.

Furthermore, if we determine the proportions for the two sorts of gametes when linkage is complete, we find them to be identical with those in table 22. This table therefore serves for the gametic proportions whether linkage is or is not complete.

(30) *Proportions of the different sorts of zygotes produced in the next generation $(n+1)$, when the breeding is by selection of recessives aa*

Here, as in (23), the selection has occurred in the production of the gametes, and the gametes now mate at random. We can therefore employ directly the table for random mating. Since however in the case of selection of recessives the gametes are the same whether linkage is complete or not, we need to employ only table 7. But as only a few of the classes of zygotes of table 7 are formed, it will simplify matters to make a new table, including only those classes. This gives us table 23. Thus the total procedure in the case of selection of recessives *aa* is as follows:

Give the proper values to the letters *c* to *l* in table 1.

Employ first the formulae of table 22.

With the results from table 22 employ the formulae of table 23. These give the proportions of the different classes of individuals in the next generation $n+1$.

(31) *Derivation of the gametes produced by the next generation $n+1$ when the gametic proportions from generation n are known*

In the very first selection the factor A was entirely excluded and can never reappear, so that no farther selection occurs, and all future breeding is by random mating. The gametes p and q thus never appear. We may therefore apply directly the gametic formulae for random mating, as given in table 9, but including only those parts based on s and t alone. This gives us:

$$s_{n+1} = (r+1)s(s+t)$$
$$t_{n+1} = (r+1)t(s+t)$$

But both the right hand members can be divided by $(r+1)(s+t)$, giving merely

$$s_{n+1} = s_n$$
$$t_{n+1} = t_n$$

that is, the proportions of s and t are constant from generation to generation; it follows that the proportions of the three possible types of gametes given in table 23 are likewise constant from generation to generation.

Thus, in the case of selection of recessives with respect to the pair A and a, we require only to obtain for the first generation the values of s and t by the formulae of table 22; these values hold for all generations. We then obtain the proportions of the zygotes by the formulae of table 23, and these values likewise hold for all generations. If we carry through in detail an analysis in the case where linkage is complete in one sex, we come to the same result.

Put in another way, selection of recessives with respect to A and a gives random mating with respect to B and b, no matter what the linkage is, and no matter whether linkage is alike in both sexes, or is complete in one sex.

IV. Assortative mating with respect to one of the pairs of characters: dominant with dominant, recessive with recessive

(32) *General.* In assortative mating with respect to a single pair of characters (as A and a), all individuals containing A mate together at random; likewise all individuals not containing the factor A. The

most interesting question involved is: What is the effect of this on a second pair of factors (*B* and *b*), that are linked with the first pair? The proportions of all possible combinations of the two pairs must of course be determined.

Assortative mating is in some sense a combination of selection for dominants on the one hand, of recessives on the other, with of course continual subtraction of the recessive products from the dominant group, and their addition to the recessive group. The chief difficulty to be met is the necessity of keeping the proportions of the two groups correct with reference to each other; they cannot be dealt with separately. This adds some complications, and to meet the difficulty certain additional designations and classifications will be introduced.

The population at the beginning is that shown in table 1. We observe that in this population the classes *c, d, g, h, i, j* and *k* contain the dominant factor *A;* it will be convenient to designate their sum by the letter *D*. The classes *e, f,* and *l* contain only the recessive factors *aa;* the sum of these three classes will be called *R*. The sum of all $(D+R)$ will be denominated *N*. For ease of reference we incorporate these in the numbered table 24.

PRODUCTION OF THE GAMETES IN ASSORTATIVE MATING

(33) For the production of gametes from the dominant zygotes (of table 1) we employ directly the formulae of table 15.

(34) For the production of gametes from the recessives we might use the formulae of table 22. It is needful, however, as will appear later, to use certain other designations for the gametic proportions in place of *s* and *t* (or *S* and *T*), in order to distinguish the gametes obtained from the recessives from those obtained from the dominants. We will therefore employ the Greek equivalents for those letters, using the lower case letters, as heretofore, for gametes formed with linkage *r,* the capital letters for those formed with complete linkage. This transforms table 22 into table 25. It will be observed that σ and Σ have the same values, as do also τ and T, but it is needful to distinguish them for the following reason. When we obtain the complete set of gametes from both dominants and recessives, one set formed with linkage *r,* the other set with complete linkage, either set may be reduced to lower terms or to decimals, independently of the other. Since the ratio of gametes derived from the dominants to those derived from the recessives is diverse in the two sets, after reduction Σ and σ may have diverse values, as may also T and τ.

(35) *Proportions of the different types of zygotes obtained from the dominants; linkage alike in both sets of gametes*

To obtain the proportions of the different classes of zygotes of generation $n + 1$, given by the mating of the gametes from the dominants of generation n, we employ directly the formulae of table 7, using of course the values of p, q, s, t obtained from table 15. To obtain correctly the final values for assortative mating it is necessary to first obtain these zygotic proportions in the forms of fractions. For this, we must divide the number in each class of zygotes by the total number of zygotes produced. This total number produced is, according to table 7, $(p+q+s+t)^2$. Furthermore, by table 15,

$$p+q+s+t = (2r+2)(c+d+g+h+i+j+k)$$

(When the letters c, d, etc., are the proportions for generation n).

Now, from this, according to table 24,

$$p+q+s+t = 2(r+1)D$$

Whence

$$(p+q+s+t)^2 = 4(r+1)^2D^2$$

So, to obtain the zygotic proportions in the form of fractions, we must divide each value of table 7 by this expression $4(r+1)^2D^2$. Thus, for example:

$$ABAB = \frac{p^2}{4(r+1)^2D^2}$$

and similarly for all the 10 classes of zygotes of table 7.

Having obtained thus the relative proportions of the different types of zygotes derived from the dominant parents, we desire to know what proportions these are of the total resulting population (derived from *both* dominant and recessive parents). Now according to table 24, the dominant parents formed the fraction D/N of all parents; their progeny will therefore form D/N of all progeny, and to obtain the proportions of the entire population formed by the various classes of these progeny, we must multiply each of these proportions by D/N. The result of this will be clear from an example. As we saw in the last paragraph, the proportion for $ABAB$ before this operation is $p^2/4(r+1)^2D^2$; multiplying this by D/N we obtain:

$$ABAB = \frac{p^2}{4(r+1)^2DN}$$

Similarly, the proportions of the total population for all the ten types of zygotes derived from the dominants will be the values given in table 7, each divided by $4(r+1)^2DN$.

(36) *Proportions of the progeny (generation $n+1$) derived from the recessives (linkage either the same in both sets or complete in one set)*

To obtain the proportions of the various types of zygotes of the next generation ($n+1$) derived from the recessives of generation n, we proceed in a manner parallel to that employed for the dominants (35). We first obtain the gametic proportion σ and τ and if needed, Σ and T from table 25. Then the proportions of the different classes of zygotes may be obtained from table 23, if we use σ and τ or Σ and T in place of s and t.

To obtain the proportions in the form of fractions, we must divide the numbers representing each class of zygotes by the total number of zygotes. By table 23 the total number of zygotes produced is $(\sigma+\tau)^2$, or $(\sigma+\tau)(\Sigma+T)$ if linkage is complete in one set, the two expressions being equivalent. By table 25,

$$\sigma+\tau=\Sigma+T=2(e+f+l),$$

and by table 24, $2(e+f+l)$ is equivalent to $2R$. Therefore the total number of zygotes produced, $(\sigma+\tau)^2$ or $(\sigma+\tau)(\Sigma+T)$ is equal to $4R^2$.

We must therefore divide each of the zygotic values in table 23 by $4R^2$. This gives the proportions that each of the classes of zygotes are of the total zygotes produced by the recessives.

To obtain in fractional form the proportions that these are of the population as a whole (derived from both dominants and recessives), we must multiply these fractions thus far obtained by the fraction that their recessive parents are of all parents; that is, by R/N. This gives the following:

	Linkage r in both sexes	Linkage complete in one sex
$e(=aBaB)=$	$\frac{\sigma^2}{4RN}$	$\frac{\Sigma\sigma}{4RN}$
$f(=abab)=$	$\frac{\tau^2}{4RN}$	$\frac{T\tau}{4RN}$
$l(=abaB)=$	$\frac{2\sigma\tau}{4RN}$	$\frac{\Sigma\tau+\sigma T}{4RN}$

Thus from the recessive parents of generation n we obtain only three sorts of zygotes of generation $n+1$, in the proportions just given.

(37) To obtain now the proportions of the population in generation $n+1$ that are formed by each of the ten possible sorts of zygotes, we must simply add the proportions derived from the dominants to those from the recessives. But only the three classes of zygotes last dealt with (*e*, *f* and *l*) require an addition from the recessives, the others being derived entirely from the dominants. Thus the proportion of $c(=ABAB)$ is $\frac{p^2}{4(r+1)^2DN}$, while that of $f(=abab)$ is $\frac{t^2}{4(r+1)^2DN} + \frac{\tau^2}{4RN}$.

Now to free our proportions from the fractional form, we must reduce them all to a common denominator. This common denominator will evidently be $4(r+1)^2RDN$. We therefore reduce all the fractions to this denominator, and conserve merely the numerators as our proportions. This gives the results shown in table 26 (column 1). These proportions can of course be at once reduced to the fractional form by dividing each by $4(r+1)^2RDN$.

(It will be observed that the only reason for the appearance of R in the values is the occurrence of R in the denominators of the table given in section (36). If we began with a population in which there were no recessives (if for example the parents were all *ABab*), then for that generation the fractions shown in the table of section (36) would not occur, and as a result no R would appear in the values of table 26. Thus if there are no recessives in generation $n(R=0)$, we do not give R the value 0 in table 26, but merely omit it entirely. If R be given the value 0 correct results will not be obtained.)

For R, D, and N only proportional values are required; thus if the values are $R=217$, $D=434$, $N=651$, we may employ simply $R=1$, $D=2$, $N=3$, since these are the proportional values.

(38) *Assortative mating; linkage complete in one sex; general formula*

When linkage is complete in one of the sets of gametes the results are to be worked out on the same principles as in the last case (32) to (37), save that for the proportions of the population produced by the dominants, we employ for the gametes both columns of table 15, followed for the zygotes by table 8. Then to obtain in fractional form the proportions from the dominants, we divide by the total number of zygotes produced from the dominants, which by table 8 is $(P+Q+S+T)(p+q+s+t)$. But by table 15

$$p+q+s+t = (2r+2)(c+d+g+h+i+j+k) = (2r+2)D \quad \text{(table 24)}$$
$$P+Q+S+T = 2(c+d+g+h+i+j+k) = 2D \quad \text{(table 24)}$$

Hence $(P+Q+S+T)(p+q+s+t) = 4(r+1)D^2$, which is the total number of zygotes produced by the dominants. We therefore divide each value in table 8 by $4(r+1)D^2$, obtaining thus the fractional proportions for the different zygotes obtained from the dominants. To determine what proportions these are of the entire population, we must, as in section (35), multiply each of these proportions by D/N. The general upshot of this division by $4(r+1)D^2$ and multiplication by D/N will be to divide each value in table 8 by $4(r+1)DN$. The proportions from the recessives will be as set forth in (36).

Next, as in (37), we reduce all the fractions to a common denominator, which in this case will be $4(r+1)RDN$. This enables us to discard the denominator, employing as the proportions of the different kinds of zygotes only their numerators. The results are given in the last column of table 26.

(39) Thus in assortative mating, to determine the proportions of the different classes of zygotes of the next generation $n+1$, when those of generation n are known, the order of procedure is as follows:

Give the proper values for the parents (generation n), to the letters c to l in table 1, and classify these parents into dominant D and recessive R, in accordance with table 24; find the proportional values of D, R, and N (of that table). These proportional values of R, D and N may be reduced or altered in any way that is convenient, provided the proportionality is maintained.

Obtain from the dominants the proportions of the different sets of gametes produced, by table 15. Thus the values of p, q, s and t are obtained; also (if required) of P, Q, S and T.

Obtain by table 25 the corresponding gametic proportions from the recessives, thus getting the values of σ and τ (and if required, of Σ and T).

Then, employing these gametic values, the proportions of the different classes of zygotes in generation $n+1$ are those shown in table 26.

By repetition of the procedure, the proportions for succeeding generations are obtainable.

See the example, section (42).

(40) *Derivation of the gametic proportions for the gametes produced by generation n+1, when those produced by n are known; assortative mating*

When we desire to obtain the zygotic proportions only for some later generation, we may shorten the procedure by working for the intervening generations only with the gametic proportions, by methods analogous to those for random mating, (12), (13) and (14), and selection of dominants (24) and (25). For this purpose we employ the values given in table 26 for the different sorts of zygotes; then determine the proportions of the different sorts of gametes produced by each,—employing in general the methods of (12), but remembering that the gametes from zygotes *e*, *f* and *l* are to be classified as σ and τ (or Σ and T).

The results are given in tables 27 and 28. In the repeated use of these tables, the values for *D* and *R* of the next generation (*n*+1) are to be found by the following equations (given in those tables):

$$p+q+s+t = (r+1)D, \text{ of generation } n+1$$
$$P+Q+S+T = D, \quad \text{of generation } n+1$$
$$\sigma+\tau \text{ (or } \Sigma+\mathrm{T}) = R, \quad \text{of generation } n+1$$

Then these values of *R* and *D* are of course to be employed in the equations for finding the gametic proportions of the next generation (see the example, section 42). Only the relative values of *R* and *D* are required; if $D = 99$ and $R = 33$, we may use $D = 3$, $R = 1$.

To find for any generation the zygotic proportions, we of course employ the results of tables 27 and 28 in table 26.

(41) *The proportions for the single factor-pairs taken separately*

One of the chief points of interest is the effect of assortative mating with respect to one pair, on the proportions of another pair linked with the former. If we mate assortatively with respect to *A* and *a*, what are the results on the proportions of the pair *B* and *b*, which are linked with *A* and *a*?

The formulae already given include all that is required for answering this question; we require merely to add together the proportions of the different zygotes that show a common constitution with respect to one of the factor pairs. For example, it is clear that *ABAB*, *AbAb*, and *ABAb* are all to be classified as *AA*, when only the pair *A* and *a* is considered. It will be well to give the formulae obtained in this way from table 26, for each pair taken separately. In table 26 it will be

observed that with respect to the pair *A* and *a*, the zygotes *c*, *d* and *i* are *AA*; *g*, *h*, *j* and *k* are *Aa*, while *e*, *f* and *l* are *aa*. With respect to *B* and *b* the zygotes *c*, *e* and *j* are *BB*; *g*, *h*, *i* and *l* are *Bb*, while *d*, *f* and *k* are *bb*. Adding the proportions accordingly, we obtain for the proportions of the single factor-pairs taken separately the values given in table 29.

For the pair *A*, *a*, table 29 will be found to give the same values as the formulae of section (15) of my former paper (JENNINGS 1916).

(42) *Example to illustrate the use of the tables for assortative mating*

Suppose that a population consists in generation 1 of 2 *ABAB* + 1 *AbAb* + 2 *aBaB* + 1 *abab* + 4 *ABab* + 3 *AbaB* + 1 *ABAb* + 2 *ABaB* + 3 *abaB*. The linkage ratio is 2(r=2), and there is assortative mating with respect to *A* and *a*.

Here, from tables 1 and 24, dominants *D* are:

$c = 2$; $d = 1$; $g = 4$; $h = 3$; $i = 1$; $j = 2$; $k = 0$; so that $D = 13$

The recessives *R* are:

$e = 2$; $f = 1$; $l = 3$; so that $R = 6$

Then from the dominants *D*, by table 15:

$p = 3(4+1+2)+4.2+3 = 32$	$P = 11$
$q = 3(2+1+0)+3.2+4 = 19$	$Q = 6$
$s = 3.2+3.2+4 = 16$	$S = 5$
$t = 3.0+4.2+3 = 11$	$T = 4$
$p+q+s+t = (2r+2)D = 78$	$P+Q+S+T = 2D = 26$

From the recessives *R*, by table 25:

$\sigma = 2.2+3 = 7$	$\Sigma = 7$
$\tau = 2.1+3 = 5$	$\mathrm{T} = 5$
$\sigma+\tau = 2R = 12$	$\Sigma+\mathrm{T} = 2R = 12$

Having thus the gametes from generation 1, we may from them find either the gametes from the next generation (2), by tables 27 and 28; or we may find at once the zygotic constitution of generation 2, by table 26. Both will be illustrated.

Gametic proportions for succeeding generations.—We shall first find the gametic proportions for the gametes derived from generation 2. Assume first that the linkage is the same (r=2) in both sets of gametes. Then by table 27 (remembering that *R* is 6 and *D* is 13).

$$p = 6.3.32.67 + 6(2.32.11 + 19.16) = 44640 = .3796$$
$$q = 6.3.19.62 + 6(2.19.16 + 32.11) = 26964 = .2772$$
$$s = 6(3.32.16 + 2.19.16 + 32.11) = 14976 = .1273$$
$$t = 6(3.19.11 + 2.32.11 + 19.16) = 9810 = .0834$$
$$p+q+s+t = 96390 = .8675$$

Therefore $D = \frac{96390}{3} = 32130$

$$\sigma = 6.16.27 + 13.3^2.7.12 = 12420 = .1056$$
$$\tau = 6.11.27 + 13.3^2.5.12 = 8802 = .0748$$
$$\sigma+\tau = 21222 = .1804$$

Therefore $R = 21222$

Total gametes $= 117612 = 1.0000$

If we desire we may reduce R and D in such a way as to make $R = 1$; that is, if we divide both by the value of R, we obtain: $R = 1$; $D = 1.513$.

Having found the proportions of the different sorts of gametes derived from generation 2, as well as R and D, for generation 2, we may now employ these values (either the entire numbers or the decimals) in finding anew the gametic proportions from generation 3, and the proportions of recessives and dominants in that generation. These may then be employed anew to find the proportions for generation 4, etc., until we reach the generation for which we wish to find the zygotic proportions.

If we assume that linkage is complete in one sex, we shall, for determining the proportions of the gametes derived from generation 2, employ table 28 in place of table 27 (used above). It is not necessary to represent the operations in detail; they will give us the following values for the proportions from the second generation:

Set 1	*Set 2*
$p = 30072$	$P = 10140$
$q = 17664$	$Q = 5772$
$s = 9834$	$S = 3162$
$t = 6690$	$T = 2346$
$p+q+s+t = 64260 = 3D \therefore D = 21420$	$P+Q+S+T = 21420 = D$
$\sigma = 8226$	$\Sigma = 8226$
$\tau = 5922$	$\mathrm{T} = 5922$
$\sigma+\tau = 14148 = R$	$\Sigma+\mathrm{T} = 14148 = R$
Total in set 1 $= 7840$	Total in set 2 $= 35568$

If $R = 1$, $D = 1.513$ (in generation 2).

The proportions in either or both sets may be reduced to smaller numbers by dividing all of the set by any number. It is not necessary that both sets should be divided by the same number. Thus set 1 may be reduced to decimals by dividing by the sum of the total for its set; set 2 by the total for that set.

Using these values (reduced or not), we may now find the proportions of the gametes from generation 3, and so on.

Zygotic proportions in any generation. By table 26 we may find the proportions of the different kinds of zygotes in generation 2 or 3, employing the gametic proportions already determined. As an illustration we will find these for generation 2 (employing the gametic values from generation 1 as given on page 131).

Linkage the same in both sets	Linkage complete in one set
c (=$ABAB$) $= 6.32^2 = 6144 = .1151$	$6.32.11 = 2112 = .1187$
d (=$AbAb$) $= 6.19^2 = 2166 = .0406$	$6.19.6 = 684 = .0384$
e (=$aBaB$) $= 6.16^2 + 13.3^2.7^2 = 7269 = .1362$	$6.5.16 + 13.3.7.7 = 2391 = .1344$
f (=$abab$) $= 6.11^2 + 13.3^2.5^2 = 3651 = .0684$	$6.4.11 + 13.3.5.5 = 1239 = .0697$
g (=$ABab$) $= 6.2.32.11 = 4224 = .0792$	$6\,(11.11+32.4) = 1494 = .0840$
h (=$AbaB$) $= 6.2.19.16 = 3648 = .0684$	$6\,(\ 6.16+19.5) = 1146 = .0707$
i(=$ABAb$) $= 6.2.32.16 = 7296 = .1367$	$6\,(11.19+32.6) = 2406 = .1353$
j (=$ABaB$) $= 6.2.32.16 = 6144 = .1151$	$6\,(11.16+32.5) = 2016 = .1133$
k (=$abAb$) $= 6.2.19.11 = 2508 = .0470$	$6\,(\ 6.11+19.4) = 852 = .0479$
l (=$abaB$) $= 6.2.16.11 + 13.3^2.2.7.5 = 10302 = .1931$	$6\,(5.11+16.4) + 13.3.(7.5+7.5) = 3444 = .1931$
Total $= 4.3^2.6.13.19 = 53352 = 1.000$	Total $= 4.3.6.13.9 = 17784 = 1.000$

Effect on the single factor-pairs taken separately. In generation 2, by table 29:

Linkage r in both sets	Linkage complete in one set
$AA = 6.51^2 = 15606 = .2925$	$6.17.51 = 5202 = .2925$
$Aa = 2.6.51.27 = 16524 = .3097$	$6.17.27 + 6.51.9 = 5508 = .3097$
$aa = 6.27^2 + 3^2.13.12^2 = 21222 = .3977$	$6.9.27 + 3.13.12.12 = 7074 = .3977$
Total $= 6.78^2 + 3^2.13.12^2 = 53352 = 1.000$	Total $= 17784 = 1.000$
$BB = 6.48^2 + 3^2.13.7^2 = 19557 = .3666$	$6.16.48 + 3.13.49 = 6519 = .3664$
$Bb = 2.6.48.30 + 2.3^2.13.7.5 = 25470 = .4774$	$6.16.30 + 6.48.10 + 3.13.70 = 8490 = .4774$
$bb = 6.30^2 + 3^2.13.5^2 = 8325 = .1560$	$6.10.30 + 3.13.25 = 2775 = .1560$
Total $= 53352 = 1.000$	Total $= 17784 = 1.000$

It will be observed that after this single assortative mating the proportions of *BB*, *Bb* and *bb* are the same whether the linkage is alike in both sets or is complete in one set; they would likewise be the same whatever the linkage, or if there were no linkage. But in later generations the proportions are diverse for different linkages, and depending on whether linkage is the same in both sets or complete in one set.

V. Self-fertilization

Thus far we have mainly used the proportions of the different types of gametes as our units, determining from these the proportions of the different sorts of zygotes, in accordance with the principle that the random mating of any set of zygotes gives the same results as the random mating of the gametes they produce. Self-fertilization differs so greatly from random mating that it is no longer convenient to base the work on this principle; we therefore deal directly with the zygotes, obtaining formulae by means of which from the zygotic proportions in earlier generations we can determine those in later generations.

In self-fertilization the linkage ratio r would perhaps be the same for both the sets of gametes produced by the single self-fertilizing individual. It is conceivable however that linkage might be found complete in the formation of one of the two sorts of gametes. We shall therefore deal, as usual, with both cases.

(43) General formula for determining the zygotic proportions in generation $n+1$, when those for generation n are known

The population at the beginning is that shown in table 1 (proper values being given to the letters c to l). These produce the gametes shown in table 3. Next the gametes produced by any single zygote mate together at random; those of column 1, table 3, in the case where linkage is the same in both sets of gametes; those of column 1 with those of column 2 (table 3), where linkage is complete in one set of gametes.

By making these matings; determining the zygotes produced (for generation $n+1$), then collecting the proportions of each kind of zygote of generation $n+1$, we obtain the formulae of table 30, giving directly the proportions of the zygotes of generation $n+1$ in terms of those of generation n. Column 1 gives the results when linkage is the same in both sets of gametes; column 2 the results when linkage is complete in one set.

Example. Let us take the example given in section (10), supposing however that breeding is by self-fertilization. That is, we begin with a population consisting of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB;* the linkage ratio r being 2. Then by table 1:

$$c = 3 \qquad f = 1 \qquad h = 1 \qquad j = 4$$

By table 30 the population in the next generation will be the following:

If linkage is the same in both sets			If linkage is complete in one set of gametes		
ABAB	$= 3^3.(12+4)+1$	$= 145 = .448$	$3\,(12+4)$	$= 48 = .444$	
AbAb	$= 2^3.1$	$= 4 = .012$	2.1	$= 2 = .019$	
aBaB	$= 3^3.4+2^3.1$	$= 40 = .123$	$3.4+2$	$= 14 = .130$	
abab	$= 3^3.4+1$	$= 37 = .114$	3.4	$= 12 = .111$	
Homozygotes		$= 226 = .698$		$= 76 = .704$	
ABab	$= 2.1$	$= 2 = .006$		$= 0 = .000$	
AbaB	$= 2.4$	$= 8 = .025$	4.1	$= 4 = .037$	
Heterozygotes		$= 10 = .031$		$= 4 = .037$	
ABAb	$= 4.1$	$= 4 = .012$		$= 1 = .009$	
ABaB	$= 2.3^3 4+4.1$	$= 76 = .235$	$2.3.4+1$	$= 25 = .231$	
abAb	$= 4.1$	$= 4 = .012$		$= 1 = .009$	
abaB	$= 4.1$	$= 4 = .012$		$= 1 = .009$	
Mixed		$= 88 = .272$		$= 28 = .259$	
Totals		$= 324 = 1.000$		$= 108 = 1.000$	

By substituting anew the values here found for the letters c to l in table 1, and reapplying the formulae of table 30, we can find if desired the proportions in generation $n + 2$, and so on for later generations. Either the actual numbers, or the proportions as reduced to decimals (the last column in each case, above) may be used for the further computations.

(44) *Special formulae for the case in which the original parents are ABab*

In this specially important case, where at the beginning of self-fertilization the parents are the result of a cross between two individuals (*ABAB* and *abab*) differing in two pairs of characters, we shall develop formulae for obtaining at once the proportions of the different sorts of zygotes after any number n of self-fertilizations.

Since we begin with *ABab,* the population is represented merely by $g = 1$ (of table 1, while all the other proportions c to l of table 1 are 0). Employing table 30 we find that after one self-fertilization ($n = 1$), the different classes of zygotes are represented as follows:

Zygotes of $n = 1$	Column 1, linkage the same ($= r$) in both sets of gametes	Column 2, linkage complete in one of the sets of gametes
c ($= ABAB$)	r^2	r
d ($= AbAb$)	1	0
e ($= aBaB$)	1	0
f ($= abab$)	r^2	r
Total homozygotes	$2r^2 + 2$	$2r$
g ($= ABab$)	$2r^2$	$2r$
h ($= AbaB$)	2	0
Total heterozygotes	$2r^2 + 2$	$2r$
i ($= ABAb$)	$2r$	1
j ($= ABaB$)	$2r$	1
k ($= abAb$)	$2r$	1
l ($= abaB$)	$2r$	1
Total mixed	$8r$	4
Grand total	$4(r+1)^2$	$4(r+1)$

Now, as we work out the proportions in later generations, we find that certain relations of equality shown in the above list hold for all generations. The four kinds of homozygotes are divisible into two pairs, those retaining the linkage of the parents (that is, c and f, or $ABAB$ and $abab$); and those not retaining the original linkage (that is d and e, or $AbAb$ and $aBaB$). The two former are always equal, and so are the two latter; that is, $c = f$, and $d = e$. Furthermore, the four kinds of mixed are always present in equal proportions. The two sorts of heterozygotes, g and h, differ in their proportional values. These relations simplify the problem, since they enable us to reduce our number of unknown quantities. Thus, instead of dealing separately with the four classes of mixed, we may find merely the total proportion of mixed (which we may call M), and we can then know that the proportion for any particular sort (as $ABaB$) will be $\frac{1}{4}$ that of M. Similar relations hold for the two sorts of homozygotes in each of the pairs. The result is that there are just five diverse quantities to deal with; the two sorts of homozygotes; the corresponding two sorts of heterozygotes, and the mixed.

In our list of the proportions of the different kinds of zygotes of generation 1 just given, each proportion is of course essentially a fraction, and its actual value is obtained by dividing the value given by the total for all; that is, by $4(r+1)^2$ in column 1, or by $4(r+1)$ in column 2. Thus in column 1 the actual fractional proportion for $g(=ABab)$ is $2r^2/4(r+1)^2$, for h it is $2/4(r+1)^2$, etc. Now,

it turns out to be most convenient to deal with certain of these proportions explicitly as fractions. The same fractions found in generation 1 occur in later generations, and it is best to designate certain of the important fractions by single letters. The fractions given by the heterozygotes turn out to be of special importance, and in particular a designation is required for the fraction given by the sum of the two sorts of heterozygotes $(g+h)$ and that given by their difference $(g—h)$. Where linkage is complete in one set, however (column 2) $g+h$ and $g—h$ are the same, since h is zero; in this case therefore we require but one designation. In column 1 (linkage $= r$ in both sets) we shall call the sum of $g+h$ by the letter v, the difference $(g—h)$ by the letter w. In column 2 (linkage complete in one set) we shall call the sum $g+h$ by the letter u; the difference $g—h$ is likewise u. That is, from the table on page 136.

Linkage $= r$ in both sets	Linkage complete in one set
$v = \frac{r^2+1}{2(r+1)^2}$ $w = \frac{r^2-1}{2(r+1)^2}$	$u = \frac{r}{2(r+1)}$

It is important to bear in mind the facts (1) that v, w and u are *fractions;* (2) that their values do not change from generation to generation, but are always those just given. It will be observed that the values for the different sorts of zygotes after one self-fertilization, as given on page 136, can be given in terms of these fractions, thus:

	Column 1	Column 2
$c = f =$	$\frac{v+w}{4}$	$\frac{u}{2}$
$d = e =$	$\frac{v-w}{4}$	0
Homozygotes $=$	v	u
$g =$	$\frac{v+w}{2}$	u
$h =$	$\frac{v-w}{2}$	0
Heterozygotes $=$	v	u
$i = j = k = l =$	$\frac{1-2v}{4}$	$\frac{1-2u}{4}$
Mixed $=$	$1-2v$	$1-2u$

(The values for the mixed result merely from the fact that they are equal to the total, minus the sum of the heterozygotes and homozygotes.)

If now we work out by table 30 the proportions of the different sorts of zygotes in later generations, and express our results in terms of the fractions v, w, and u, we discover for any generation n the following general relations:

	Linkage = r in both sets	Linkage complete in one set
Sum of the two classes of homozygotes, $(c+f)+(d+e)$	$= \frac{2^{n-2}}{2^n} + v^n$	$\frac{2^{n-2}}{2^n} + u^n$
Difference of the two classes of homozygotes, $(c+f)-(d+e)$	$= w^1+w^2+w^3 \ldots w^n$	$u^1+u^2+u^3 \ldots u^n$
Sum of the two classes of heterozygotes, $g+h$	$= v^n$	u^n
Difference of the two classes of heterozygotes, $g-h$	$= w^n$	u^n

These equations may readily be solved for the values of $c+f$ and of $d+e$; also for the values of g and h. Since we know that $c=f$ and $d=e$, this will give us at once the values of c, d, e, f, g and h. We can, of course, then readily obtain the value of the total mixed (since these constitute merely the remainder) and of any particular class of mixed (since the four classes of mixed are equal). Carrying out these solutions, we obtain the final formulae set forth in table 31.

Example. Let us suppose that, beginning with the parent *ABab*, there have been three self-fertilizations; that the linkage ratio is 2; and that linkage is the same in both sets of gametes.

Here we have:

$$r=2 \qquad v=\tfrac{5}{18} \qquad u=\tfrac{3}{18} \qquad n=3$$

Hence:

Total homozygotes $= \frac{2^2-1}{2^2} + (\frac{5}{18})^3 = \frac{3}{4} + \frac{125}{5832} = \frac{4499}{5832} = .7714$

$c(=ABAB) = \frac{2^2-1}{2^4} + \frac{1}{4}[(\frac{5}{18})^3 + (\frac{3}{18})^3 + (\frac{3}{18})^2 + \frac{3}{18}] = \frac{1415}{5832} = .2427$

$d(=AbAb) = \frac{2^2-1}{2^4} + \frac{1}{4}[(\frac{5}{18})^3 - (\frac{3}{18})^3 - (\frac{3}{18})^3 - \frac{3}{18}] = \frac{1669}{11664} = .1431$

$e(=aBaB) = .1431$

$f(=abab) = .2427$

Total heterozygotes $= (\frac{5}{18})^3 = \frac{125}{5832} = .0214$

$g(=ABab) = \frac{1}{2}[(\frac{5}{18})^3 + (\frac{3}{18})^3] = \frac{76}{5832} = .0130$

$h(=AbaB) = \frac{1}{2}[(\frac{5}{18})^3 - (\frac{3}{18})^3] = \frac{49}{5832} = .0084$

Total mixed $= \frac{1}{4} - 2(\frac{5}{18})^3 = \frac{1208}{5832} = .2071$

Any single class of mixed (as *ABAb*) $= \frac{1}{4} \times \frac{1208}{5832} = .0518$

If we assume that linkage is complete in one of the sets of gametes, we have $u = 1/3$; the results are then obtained in a similar manner; they are as follows:

$$\text{Total homozygotes} = .7870$$
$$d = e = .0764$$
$$c = f = .3171$$

$$\text{Total heterozygotes} = (1/3)^3 = 1/27 = .0370$$
$$g(= ABab) = (1/3)^3 = .0370$$
$$c = f = .3171$$

$$\text{Total mixed} = 1/2^2 - 2(1/3)^3 = 38/216 = .1759$$
$$\text{Any single class of mixed, as } ABaB = (1/2)^4 - 1/2(1/3)^3 = .0439$$

If we classify the results with respect to either of the single pairs of factors (as *A* and *a*), we of course obtain the same results given in section (25) of my previous paper (JENNINGS 1916), that is:

$$AA \text{ (or } BB) = \frac{2^n - 1}{2^{n+1}}$$

$$aa \text{ (or } bb) = \frac{2^n - 1}{2^{n+1}}$$

$$Aa \text{ (or } Bb) = \frac{1}{2^n}$$

(45) *Parents AbaB (derived from a cross of AbAb with aBaB)*

In this case, the results are as given in table 31, but with the following alterations in the formulae:

The values for *c* and *d* are to be interchanged.

The values for *e* and *f* are to be interchanged.

The values for *g* and *h* are to be interchanged.

The values remain unchanged for the total homozygotes; for the total heterozygotes; for the total mixed; and for any particular class of mixed.

REMARKS ON INBREEDING. To obtain a general formula for inbreeding with brother by sister mating, when two linked pairs of characters are considered, one begins with a family composed as in table 1, proper values being given to the letters *c* to *l*. When such a family is inbred, the linkage ratio being *r* for both sexes, it gives 55 diverse types of families (the number of families being $\frac{n(n+1)}{2}$ where *n* is the number

of differing individuals in the original family). By determining the types of families produced from each of these 55 families, and collecting the results for each of the possible 55 kinds of newly formed families, one obtains formulae giving the constitution in families in the generation $n + 1$, when that in generation n is known. Such formulae are complex, some of the 55 equations being made up of as many as 24 terms. It hardly seems worth while to publish the complex table of formulae thus obtained; possibly it may be employed later to obtain the actual gametic constitution of the population in later generations for the more important special cases, as when the original parents are all *ABab*, and the like. The entire subject of inbreeding with relation to two pairs of linked factors is therefore reserved for further treatment. The paper of DETLEFSEN (1914) contains discussions and formulae for certain special cases of inbreeding when two pairs of independent factors are dealt with. The present writer would find it a relief if some one else would deal thoroughly with the laborious problem of the effects of inbreeding on two pairs of linked factors.

SUMMARY

This paper derives formulae for finding in later generations the results of continued breeding by a given system, when two pairs of characters, linked or independent, are considered. Its primary purpose is to render it possible to determine the effects of linkage on the distribution of the factors. The systems of breeding considered are: random mating; selection with respect to a given single character; assortative mating with respect to a single character; and self-fertilization. In each system two cases are dealt with; that in which linkage is the same in both sets of gametes; and that in which linkage is complete in one set. In each system general formulae are derived for transforming generation n into generation $n + 1$. In several systems special formulae are given for finding directly in any later generation n the proportions of the population, when one begins with parents that are a cross between *ABAB* and *abab*; or between *AbAb* and *aBaB*. With regard to selection and assortative mating with respect to a single character, formulae are given for the effect on the single pairs taken separately; thus for the effect of selection or assortative mating with respect to one character on the distribution of another character linked with that one.

The formulae are collected for convenience in 31 tables, which are placed in order at the end of the paper.

LITERATURE CITED

DETLEFSEN, J. A., 1914 Genetic studies on a cavy species cross. Carnegie Institution of Washington, Publication No. 205, 134 pp.

JENNINGS, H. S., 1916 The numerical results of diverse systems of breeding. Genetics **1**: 53-89.

WENTWORTH, E. N., and REMICK, B. L., 1916 Some breeding properties of the generalized Mendelian population. Genetics **1**: 608-616.

TABLES FOR USE IN COMPUTING THE NUMERICAL RESULTS OF DIVERSE SYSTEMS OF BREEDING, WITH RESPECT TO TWO PAIRS OF FACTORS

Table 1. The ten diverse possible classes of zygotes with respect to two pairs of factors (*A, a* and *B, b*), with the algebraic designations (*c* to *l*) that will be employed to represent their respective proportions. By giving the proper values to the letters *c* to *l*, any population may be represented by this table.

Homozygotes	*Heterozygotes*	*Mixed*
c.ABAB	*g.ABab*	*i.ABAb*
d.AbAb	*h.AbaB*	*j.ABaB*
e.aBaB		*k.abAb*
f.abab		*l.abaB*

With respect to the single pairs taken separately:

$AA = c+d+i$	$aa = e+f+l$	$Aa = g+h+j+k$
$BB = c+e+j$	$bb = d+f+k$	$Bb = g+h+i+l$

Table 2. The four possible classes of gametes with respect to two pairs of factors, with the algebraic designations (*p, q, s, t*) for their relative proportions.

p.AB	*q.Ab*	*s.aB*	*t.ab*

(To distinguish certain classes of gametes, in some cases the capital letters, *P, Q, S, T,* will be used in place of the lower case letters; and in assortative mating, for special purposes the corresponding Greek letters σ and τ will be used for *s* and *t*. See tables 5, 8, 25, 26, etc.)

Table 3. Gametes given by the ten sorts of zygotes of table 1, when the linkage is r; and when linkage is complete.

Zygotes	Gametes produced	
	1. Linkage $= r$	2. Linkage complete
$c.ABAB$	$c.(2r+2)AB$	$2c.AB$
$d.AbAb$	$d.(2r+2)Ab$	$2d.Ab$
$e.aBaB$	$e.(2r+2)aB$	$2e.aB$
$f.abab$	$f.(2r+2)ab$	$2f.ab$
$g.ABab$	$g.(r\,AB+1\,Ab+1\,aB+r\,ab)$	$g.AB+g.ab$
$h.AbaB$	$h.(r\,Ab+1\,AB+1\,ab+r\,aB)$	$h.Ab+h.aB$
$i.ABAb$	$i.(r+1)AB+i.(r+1)Ab$	$i.AB+i.Ab$
$j.ABaB$	$j.(r+1)AB+j.(r+1)aB$	$j.AB+j.aB$
$k.abAb$	$k.(r+1)ab+k.(r+1)Ab$	$k.ab+k.Ab$
$l.abaB$	$l.(r+1)ab+l.(r+1)aB$	$l.ab+l.aB$

Table 4. Linkage r. Proportions of the different kinds of gametes produced by a population of zygotes (of table 1) in terms of the proportions of the zygotes.

$$p(=AB) = (r+1)(2c+i+j)+rg+h$$
$$q(=Ab) = (r+1)(2d+i+k)+rh+g$$
$$s(=aB) = (r+1)(2e+j+l)+rh+g$$
$$t(=ab) = (r+1)(2f+k+l)+rg+h$$
$$p+q+s+t = (2r+2)(c+d+e+f+g+h+i+j+k+l)$$

Table 5. Linkage complete. Proportions of the different kinds of gametes produced by a population of zygotes (table 1), in terms of the proportions of the parent zygotes.

$$P(=AB) = 2c+g+i+j$$
$$Q(=Ab) = 2d+h+i+k$$
$$S(=aB) = 2e+h+j+l$$
$$T(=ab) = 2f+g+k+l$$
$$P+Q+S+T = 2(c+d+e+f+g+h+i+j+k+l)$$
$$p+q+s+t \text{ (of table 4)} = (r+1)(P+Q+S+T)$$

Table 6. Random mating of the four types of gametes (of table 2), with the zygotes produced.

Gametes		*Gametes*		*Zygotes*			
p. AB	×	*p. AB*	=	$p.^2$ *AB* / *AB*	*pq. AB* / *Ab*	*ps. AB* / *aB*	*pt. AB* / *ab*
q. Ab		*q. Ab*		*qp. Ab* / *AB*	$q.^2$ *Ab* / *Ab*	*qs. Ab* / *aB*	*qt. Ab* / *ab*
s. aB		*s. aB*		*sp. aB* / *AB*	*sq. aB* / *Ab*	$s.^2$ *aB* / *aB*	*st. aB* / *ab*
t. ab		*t. ab*		*tp. ab* / *AB*	*tq. ab* / *Ab*	*ts. ab* / *aB*	$t.^2$ *ab* / *ab*

Table 7. Proportions of the various types of zygotes resulting from the random mating of the four types of gametes (of tables 2 and 6), in terms of the proportions of the gametes.

Homozygotes

$c(=ABAB) = p^2$
$d(=AbAb) = q^2$
$e(=aBaB) = s^2$
$f(=abab) = t^2$

Mixed

$i(=ABAb) = 2pq$
$j(=ABaB) = 2ps$
$k(=abAb) = 2qt$
$l(=abaB) = 2st$

Total homozygotes $= p^2+q^2+s^2+t^2$. Total mixed $= 2(pq+ps+qt+st)$

Heterozygotes

$g(=ABab) = 2pt$
$h(=AbaB) = 2qs$

Total heterozygotes $= 2(pt+qs)$

Total zygotes $= (p+q+s+t)^2$

Table 8. Proportions of the various types of zygotes resulting from the random mating of the four types of gametes produced with linkage r (table 4), with the four types produced with complete linkage (table 5).

Homozygotes

$c(=ABAB) = Pp$
$d(=AbAb) = Qq$
$e(=aBaB) = Ss$
$f(=abab) = Tt$

Total homozygotes $= Pp+Qq+Ss+Tt$

Mixed

$i(=ABAb) = Pq+pQ$
$j(=ABaB) = Ps+pS$
$k(=abAb) = Qt+qT$
$l(=abaB) = St+sT$

Total mixed $= Pq+pQ+Ps+pS+Qt+qT+St+sT$

Heterozygotes

$g(=ABab) = Pt+pT$
$h(=AbaB) = Qs+qS$

Total heterozygotes $= Pt+pT+Qs+qS$

Total zygotes $= (P+Q+S+T)(p+q+s+t)$

Table 9. Random mating, linkage the same ($=r$) in both sets of gametes. Formulae for the proportions of the gametes derived from generation $n+1$ (therefore *producing* generation $n+2$), in terms of the gametes derived from generation n (and therefore producing generation $n+1$). That is, formulae for p_{n+1}, q_{n+1}, s_{n+1}, t_{n+1}, in terms of p_n, q_n, s_n, t_n.

Gametes from generation $n+1$		In terms of gametes from generation n
$p(=AB)$	=	$(r+1)p(p+q+s)+rpt+qs$
$q(=Ab)$	=	$(r+1)q(p+q+t)+rqs+pt$
$s(=aB)$	=	$(r+1)s(p+s+t)+rqs+pt$
$t(=ab)$	=	$(r+1)t(q+s+t)+rpt+qs$
$p+q+s+t$	=	$(r+1)(p+q+s+t)^2$

Table 10. Random mating; independent factors (no linkage). Proportions of the different kinds of gametes derived from generation $n+1$, in terms of those derived from generation n. This is table 9, simplified for the case of no linkage ($r=1$).

Gametes from $n+1$		In terms of gametes from n
$p(=AB)$	=	$2p(p+q+s)+pt+qs$
$q(=Ab)$	=	$2p(p+q+t)+qs+pt$
$t(=ab)$	=	$2t(q+s+t)+pt+qs$
$s(=aB)$	=	$2s(p+s+t)+qs+pt$
$p+q+s+t$	=	$2(p+q+s+t)^2$

Table 11. Random mating; linkage complete in one set of gametes, r in the other. Formulae for the proportions of the two sets of gametes derived from generation $n+1$, in terms of the gametic proportions of the two sets derived from generation n.

Gametes from $n+1$	In terms of gametes from n
	Set 1. Gametes with linkage r.
$p(=AB)$ =	$(r+1)p(P+Q+S)+(r+1)P(p+q+s)+r(Pt+pT)+Qs+qS$
$q(=Ab)$ =	$(r+1)q(P+Q+T)+(r+1)Q(p+q+t)+r(Qs+qS)+Pt+pT$
$s(=aB)$ =	$(r+1)s(P+S+T)+(r+1)S(p+s+t)+r(Qs+qS)+Pt+pT$
$t(=ab)$ =	$(r+1)t(Q+S+T)+(r+1)T(q+s+t)+r(Pt+pT)+Qs+qS$
$p+q+s+t$ =	$2(r+1)(P+Q+S+T)(p+q+s+t)$
	Set 2. Gametes with complete linkage
$P(=AB)$ =	$P(p+q+s+t)+p(P+Q+S+T)$
$Q(=Ab)$ =	$Q(p+q+s+t)+q(P+Q+S+T)$
$S(=aB)$ =	$S(p+q+s+t)+s(P+Q+S+T)$
$T(=ab)$ =	$T(p+q+s+t)+t(P+Q+S+T)$
$P+Q+S+T$ =	$2(P+Q+S+T)(p+q+s+t)$

Table 12. Random mating, linkage complete in one set of gametes, r in the other set. Certain relations between the proportions of the gametes of the two sets, in any given generation. Derived from table 11.

(The same relations hold for the two sets of table 15, in selection for dominants.)

Set 1	*Set 2*
$p+q$ =	$(r+1)(P+Q)$
$p+s$ =	$(r+1)(P+S)$
$q+t$ =	$(r+1)(Q+T)$
$s+t$ =	$(r+1)(S+T)$
$p+q+s+t$ =	$(r+1)(P+Q+S+T)$

Table 13. Random mating, original parents all *ABab;* linkage r in both sets of gametes. Proportions of the different classes of gametes for producing any required generation n.

Gametes for producing generation n		
$p(=t)$	=	$(r+1)^n+r^n-r^{n-1}$
$q(=s)$	=	$(r+1)^n-r^n+r^{n-1}$

If the original parents are *AbaB*, interchange the values of $p(=t)$ and $q(=s)$.

Table 14. Random mating, original parents all *ABab;* linkage r in one set of gametes, complete in the other. Proportions of the different classes of gametes for producing any required generation n.

Gametes for producing generation n		
$p(=t)$	=	$2^{n-2}(r+1)^n+r^2(2r+1)^{n-2}$
$q(=s)$	=	$2^{n-2}(r+1)^n-r^2(2r+1)^{n-2}$
$P(=T)$	=	$2^{n-2}(r+1)^{n-1}+r(2r+1)^{n-2}$
$Q(=S)$	=	$2^{n-2}(r+1)^{n-1}-r(2r+1)^{n-2}$

If the original parents are *AbaB,* interchange the values of $p(=t)$ and $q(=s)$; also interchange the values of $P(=T)$ and $Q(=S)$.

Table 15. Selection for dominant A. Proportions of the different kinds of gametes produced by a population of zygotes (of table 1), in terms of the proportions of the zygotes; when linkage is r; and when it is complete.

Set 1. Linkage r	Set 2. Linkage complete
$p(=AB) = (r+1)(2c+i+j)+rg+h$	$P(=AB) = 2c+g+i+j$
$q(=Ab) = (r+1)(2d+i+k)+rh+g$	$Q(=Ab) = 2d+h+i+k$
$s(=aB) = (r+1)j+rh+g$	$S(=aB) = h+j$
$t(=ab) = (r+1)k+rg+h$	$T(=ab) = g+k$
$p+q+s+t = (2r+2)(c+d+g+h+i+j+k)$	$P+Q+S+T = 2(c+d+g+h+i+j+k)$

The relations shown in table 12 hold for the two sets of table 15, as well as for those of table 11.

Table 16. Selection for dominant A; linkage the same $(=r)$ in both sets of gametes. Proportions of the different sorts of gametes derived from generation $n+1$, in terms of those derived from generation n.

Gametes produced by generation $n+1$		In terms of gametes produced by generation n
$p(=AB)$	=	$(r+1)p(p+q+s)+rpt+qs$
$q(=Ab)$	=	$(r+1)q(p+q+t)+rqs+pt$
$s(=aB)$	=	$(r+1)ps+rqs+pt$
$t(=ab)$	=	$(r+1)qt+rpt+qs$
$p+q+s+t$	=	$(r+1)(p+q)(p+q+s+t)$

Table 17. Selection of dominant A; linkage complete in one set of gametes; r in the other. Proportions of the two sets of gametes derived from generation $n+1$, in terms of the gametic proportions of the two sets derived from generation n.

Set 1. Gametes with linkage r

Gametes from

$n+1$	In terms of gametes from n
$p(=AB) =$	$(r+1)p(P+Q+S)+(r+1)P(p+q+s)+r(Pt+pT)+Qs+qS$
$q(=Ab) =$	$(r+1)q(P+Q+T)+(r+1)Q(p+q+t)+r(Qs+qS)+Pt+pT$
$s(=aB) =$	$(r+1)(Sp+sP)+r(Qs+qS)+Pt+pT$
$t(=ab) =$	$(r+1)(Qt+qT)+r(Pt+pT)+Qs+qS$
$p+q+s+t =$	$2(r+1)[(p+q)(P+Q+S+T)+(P+Q)(s+t)]$

Set 2. Gametes with complete linkage

$$P(=AB) = P(p+q+s+t)+p(P+Q+S+T)$$
$$Q(=Ab) = Q(p+q+s+t)+q(P+Q+S+T)$$
$$S(=aB) = S(p+q)+s(P+Q)$$
$$T(=ab) = T(p+q)+t(P+Q)$$
$$P+Q+S+T = 2[(p+q)(P+Q+S+T)+(P+Q)(s+t)]$$

Table 18. Proportions of the gametes containing A or a; and of those containing B or b. (In terms of tables 9 to 11, or of tables 15 to 17; these relations of course hold equally of random mating and of selection of dominants.)

Set 1. Gametes with linkage r	Set 2. Gametes with complete linkage
$A = p + q$	$A = P + Q$
$a = s + t$	$a = S + T$
$B = p + s$	$B = P + S$
$b = q + t$	$b = Q + T$

Table 19. Proportions of the different classes of zygotes in generation $n+1$, with reference to the single factor-pairs taken separately, in terms of the gametes of tables 9 to 11 or of tables 15 to 17.

Set 1. Linkage (r) the same in both sets of gametes	Set 2. Linkage complete in one set of gametes; r in the other
$AA = (p+q)^2$	$AA = (p+q)(P+Q)$
$Aa = 2(p+q)(s+t)$	$Aa = (p+q)(S+T)+(P+Q)(s+t)$
$aa = (s+t)^2$	$aa = (s+t)(S+T)$
$BB = (p+s)^2$	$BB = (p+s)(P+S)$
$Bb = 2(p+s)(q+t)$	$Bb = (p+s)(Q+T)+(P+S)(q+t)$
$bb = (q+t)^2$	$bb = (q+t)(Q+T)$

Table 20. Selection of parents containing dominant *A*. Original parents all *ABab*. Proportions of the 10 possible sorts of individuals (zygotes) produced for the first 4 generations (n) when there is no linkage ($r=1$), when the linkage ratio is 2 in both sexes ($r=2$), and when the linkage is 2 in one sex, but complete in the other ($r=2+$).

$n=$	1			2		
$r=1$	2	2+	1	2	2+
ABAB = 1=.0625	4=.1111	2=.1667	4=.1111	121=.1670	260=.2675
AbAb = 1=.0625	1=.0278	0=.0	4=.1111	49=.0672	20=.2058
aBaB = 1=.0625	1=.0278	0=.0	1=.0278	16=.0219	7=.0072
abab = 1=.0625	4=.1111	2=.1667	1=.0278	25=.0343	55=.0566
Homo. = 4=.2500	10=.2778	4=.3333	10=.2778	211=.2894	342=.3519
ABab = 2=.1250	8=.2222	4=.3333	4=.1111	110=.1509	240=.2469
AbaB = 2=.1250	2=.0555	0=.0	4=.1111	56=.0768	24=.0247
Hetero. = 4=.2500	10=.2778	4=.3333	8=.2222	166=.2277	264=.2716
ABAb = 2=.1250	4=.1111	1=.0833	8=.2222	154=.2112	152=.1564
ABaB = 2=.1250	4=.1111	1=.0833	4=.1111	88=.1207	96=.0988
abAb = 2=.1250	4=.1111	1=.0833	4=.1111	70=.0960	72=.0741
abaB = 2=.1250	4=.1111	1=.0833	2=.0555	40=.0549	46=.0473
Mixed = 8=.5000	16=.4444	4=.3333	18=.5000	352=.4829	366=.3765
Total =16=1.	36=1.	12=1.	36=1.	729=1.	972=1.

$n=$	3		4		
$r=1$	2	2+	1	2	2+
ABAB = 9=.1406	1024=.1975	1638=.3160	16=.1600	143,641=.2189	33,480=.3444
AbAb = 9=.1406	484=.0934	180=.0347	16=.1600	72,361=.1103	4,392=.0452
aBaB = 1=.0156	81=.0156	40=.0077	1=.0100	7,396=.0113	689=.0071
abab = 1=.0156	81=.0156	130=.0251	1=.0100	5,776=.0088	1,205=.0130
Homo. =20=.3125	1670=.3221	1938=.3738	34=.3400	229,174=.3493	39,826=.4097
ABab = 6=.0937	576=.1111	927=.1788	8=.0800	57,608=.0878	13,070=.1345
AbaB = 6=.0937	396=.0764	171=.0330	8=.0800	46,268=.0705	3,494=.0359
Hetero.=12=.1875	972=.1875	1098=.2118	16=.1600	103,876=.1583	16,564=.1704
ABAb =18=.2813	1408=.2716	1098=.2118	32=.3200	203,902=.3107	24,336=.2504
ABaB = 6=.0937	576=.1111	531=.1024	8=.0800	65,188=.0993	9,754=.1003
abAb = 6=.0937	396=.0764	315=.0608	8=.0800	40,888=.0623	4,786=.0492
abaB = 2=.0313	162=.0312	154=.0297	2=.0200	13,072=.0199	1,934=.0199
Mixed =32=.5000	2542=.4904	2098=.4049	50=.5000	323,050=.4923	40,810=.4199
Total =64=1.	5184=1.	5184=1.	100=1.	656,100=1.	97,200=1.

Table 21. Selection of parents containing dominant *A*. Original parents all *ABab*. Proportions of the different sorts of individuals for the single factor pairs taken separately, for the first four generations of selection, when there is no linkage ($r=1$); when the linkage ratio is 2 in both sexes ($r=2$), and when the linkage is 2 in one sex but complete in the other ($r=2+$). Primarily to illustrate the effect of selection with respect to one factor-pair (*A*, *a*) on another factor-pair (*B*, *b*), linked with the former, or independent of it.

n =	1		2		
r = 1	2	2+	1	2	2+
AA = 1	1	1	4	4	4
Aa = 2	2	2	4	4	4
aa = 1	1	1	1	1	1
Totals 4	4	4	9	9	9
BB = 1	1	1	1	25	121
Bb = 2	2	2	2	40	154
bb = 1	1	1	1	16	49
Totals 4	4	4	4	81	324
n =	3			4	
r = 1	2	2+	1	2	2+
AA = 9	9	9	16	16	16
Aa = 6	6	6	8	8	8
aa = 1	1	1	1	1	1
Totals 16	16	16	25	25	25
BB = 1	1681	2209	1	961	14641
Ab = 2	2542	2350	2	1426	14278
bb = 1	961	625	1	529	3481
Totals 4	5184	5184	4	2916	32400

Table 22. Selection of recessive *aa;* linkage either r, or complete. Proportions of the different kinds of gametes produced by a population (table 1), in terms of the proportions of the zygotes given in table 1.

$$s \text{ or } S(=aB) = 2e+l$$
$$t \text{ or } T(=ab) = 2f+l$$
$$s+t \text{ (or } S+T) = 2(e+f+l)$$

Table 23. Selection of recessive *aa;* linkage either r in both sets of gametes, or complete in one set. Proportions of the different classes of zygotes, in any generation n, in terms of the gametes (table 22) from generation 1.

$$\begin{aligned} e(=aBaB) &= s^2 \quad (\text{or } sS) \\ f(=abab) &= t^2 \quad (\text{or } tT) \\ l(=abaB) &= 2st \quad (\text{or } sT+St) \\ \text{Total zygotes } (e+f+l) &= (s+t)^2, \ (\text{or } (s+t)(S+T)) \end{aligned}$$

Table 24. Assortative mating. Designations to be employed for the sums of the classes of zygotes of table 1 that are dominant (D) with respect to the character A; that are recessive (R) with respect to that character; and for the sum of all (N). In terms of the proportions given in table 1.

$$\begin{aligned} D &= c+d+g+h+i+j+k \\ R &= e+f+l \\ N &= D+R \end{aligned}$$

Table 25. Assortative mating. Proportions of the different kinds of gametes produced by the recessives (aa) of a population (table 1), in terms of the zygotes producing them. (This table is the same as table 22, but with substitution of Greek letters for the corresponding English ones, for the exigencies of work with assortative mating.)

Set 1. Gametes formed with linkage r

$$\begin{aligned} \sigma(=aB) &= 2e+l \\ \tau(=ab) &= 2f+l \\ \sigma+\tau &= 2(e+f+l) \end{aligned}$$

Set 2. Gametes formed with complete linkage

$$\begin{aligned} \Sigma(=aB) &= 2e+l \\ \mathrm{T}(=ab) &= 2f+l \\ \Sigma+\mathrm{T} &= 2(e+f+l) \end{aligned}$$

Table 26. Assortative mating. Proportions of the different classes of zygotes in the next generation $n+1$, in terms of the gametes producing them (of tables 15 and 25), and of the proportions of D, R, and N of table 24.

N. B. Where R is 0, simply omit R from the values; do *not* give R the value of 0 (see note in section (37)). For R, D and N any values that conserve their correct relative proportions may be employed.

Zygotes of $n+1$	Column 1. Proportions when the linkage (r) is the same in both sets of gametes	Column 2. Proportions when the linkage is complete in one set of gametes, r in the other
$c(=ABAB)$	Rp^2	$R\,Pp$
$d(=AbAb)$	Rq^2	$R\,Qq$
$e(=aBaB)$	$Rs^2+D(r+1)^2\sigma^2$	$R\,Ss+D(r+1)\Sigma\sigma$
$f(=abab)$	$Rt^2+D(r+1)^2\tau^2$	$R\,Tt+D(r+1)\mathrm{T}\tau$
$g(=ABab)$	$2Rpt$	$R(Pt+pT)$
$h(=AbaB)$	$2Rqs$	$R(Qs+qS)$
$i(=ABAb)$	$2Rpq$	$R(Pq+pQ)$
$j(=ABaB)$	$2Rps$	$R(Ps+pS)$
$k(=abAb)$	$2Rqt$	$R(Qt+qT)$
$l(=abaB)$	$2Rst+2(r+1)^2D\sigma\tau$	$R(St+sT)+D(r+1)(\Sigma\tau+\sigma\mathrm{T})$

Table 27. Assortative mating. Linkage (r) the same in both sets of gametes. Formulae for deriving the proportions of the different kinds of gametes produced by generation $n+1$, when the gametes produced by generation n are known.

N. B. Where R is 0 it is to be omitted from the equations; *not* given the value 0.

(1) From the dominants

Gametes from $n+1$		In terms of gametes from n, and of R and D of generation n
$p(=AB)$	$=$	$R(r+1)p(p+q+s)+R(rpt+qs)$
$q(=Ab)$	$=$	$R(r+1)q(p+q+t)+R(rqs+pt)$
$s(=aB)$	$=$	$R[(r+1)ps+rqs+pt]$
$t(=ab)$	$=$	$R[(r+1)qt+rpt+qs]$

(2) From the recessives

$$\sigma(=aB) = Rs(s+t)+D(r+1)^2\sigma(\sigma+\tau)$$
$$\tau(=ab) = Rt(s+t)+D(r+1)^2\tau(\sigma+\tau)$$

$$D_{n+1} = \frac{p+q+s+t}{r+1} \text{ of generation n+1}$$

$$R_{n+1} = \sigma+\tau \text{ of generation } n+1$$

Table 28. Assortative mating; linkage complete in one set of gametes, r in the other. Formulae for the gametes produced by generation $n+1$, in terms of those produced by generation n.

N. B. Where R is 0, the factor R is to be omitted from the equations. It must *not* be given the value 0.

Set 1. From the sex in which linkage is r.

(1) From the dominants

Gametes from $n+1$ — In terms of gametes from n, and of R and D of n

$$p(=AB) = R(r+1)P(p+q+s)+R(r+1)p(P+Q+S)+R(rPt+rpT+Qs+qS)$$
$$q(=Ab) = R(r+1)Q(p+q+t)+R(r+1)q(P+Q+T)+R(rQs+rqS+Pt+pT)$$
$$s(=aB) = R(r+1)(Ps+pS)+R(rQs+rqS+Pt+pT)$$
$$t(=ab) = R(r+1)(Qt+qT)+R(rPt+rpT+Qs+qS)$$

(2) From the recessives

$$\sigma(=aB) = R(2Ss+St+sT)+D(r+1)(2\Sigma\sigma+\Sigma\tau+\sigma T)$$
$$\tau(=ab) = R(2Tt+St+sT)+D(r+1)(2T\tau+\Sigma\tau+\sigma T)$$

Set 2. From the sex with linkage complete.

(1) From the dominants

$$P(=AB) = RP(p+q+s+t)+Rp(P+Q+S+T)$$
$$Q(=Ab) = RQ(p+q+s+t)+Rq(P+Q+S+T)$$
$$S(=aB) = RS(p+q)+Rs(P+Q)$$
$$T(=ab) = RT(p+q)+Rt(P+Q)$$

(2) From the recessives

$$\Sigma(=aB) = R(2Ss+St+sT)+D(r+1)(2\Sigma\sigma+\Sigma\tau+\sigma T)$$
$$T(=ab) = R(2Tt+St+sT)+D(r+1)(2T\tau+\Sigma\tau+\sigma T)$$
$$D_{n+1} = P+Q+S+T = \frac{p+q+s+t}{r+1} \text{ (of generation } n+1)$$
$$R_{n+1} = \sigma+\tau = \Sigma+T \text{ (of generation } n+1)$$

Table 29. Assortative mating. Proportions of the different classes of zygotes in generation $n+1$, with respect to the two pairs of factors taken separately, in terms of the gametes from generation n, and of R and D of generation n. Derived from table 26.

Zygotes	Column 1. Proportions when the linkage is the same (r) in both sets of gametes.	Column 2. Proportions when the linkage is complete in one set, r in the other set of gametes.
$AA(=c+d+i)$	$R(p+q)^2$	$R(P+Q)(p+q)$
$Aa(=g+h+j+k)$	$2R(p+q)(s+t)$	$R(P+Q)(s+t)+R(p+q)(S+T)$
$aa(=e+f+l)$	$R(s+t)^2+(r+1)^2D(\sigma+\tau)^2$	$R(S+T)(s+t)+(r+1)D(\Sigma+\mathbf{T})(\sigma+\tau)$
Total	$R(p+q+s+t)^2+(r+1)^2D(\sigma+\tau)^2$	$R(P+Q+S+T)(p+q+s+t)+(r+1)D(\Sigma+\mathbf{T})(\sigma+\tau)$
$BB(=c+e+j)$	$R(p+s)^2+(r+1)^2D\sigma^2$	$R(P+S)(p+s)+(r+1)D\Sigma\sigma$
$Bb(=g+h+i+l)$	$2R(p+s)(q+t)+2(r+1)^2D\sigma\tau$	$R(P+S)(q+t)+R(p+s)(Q+T)+(r+1)D(\Sigma\tau+\sigma\mathbf{T})$
$bb(=d+f+k)$	$R(q+t)^2+(r+1)^2D\tau^2$	$R(Q+T)(q+t)+(r+1)D\tau\mathbf{T}$
Total	$R(p+q+s+t)^2+(r+1)^2D(\sigma+\tau)^2$	$R(P+Q+S+T)(p+q+s+t)+(r+1)D(\Sigma+\mathbf{T})(\sigma+\tau)$

Table 30. Self-fertilization; proportions of the different kinds of zygotes in generation $n+1$, in terms of their proportions in generation n (the proportions in generation n are those given in table 1). Column 1, results when linkage is the same in both sets of gametes; column 2, when linkage is complete in one set.

Zygotes of $n+1$	In terms of proportions of zygotes of generation n	
	1. Linkage the same in both sets	2. Linkage complete in one set
$c(=ABAB)$	$(r+1)^2(4c+i+j)+r^2g+h$	$(r+1)(4c+i+j)+rg$
$d(=AbAb)$	$(r+1)^2(4d+i+k)+r^2h+g$	$(r+1)(4d+i+k)+rh$
$e(=aBaB)$	$(r+1)^2(4e+j+l)+r^2h+g$	$(r+1)(4e+j+l)+rh$
$f(=abab)$	$(r+1)^2(4f+k+l)+r^2g+h$	$(r+1)(4f+k+l)+rg$
Total homozygotes	$2(r+1)^2(2c+2d+2e+2f+i+j+k+l)+2(r^2+1)(g+h)$	$2(r+1)(2c+2d+2e+2f+i+j+k+l)+2r(g+h)$
$g(=ABab)$	$2(r^2g+h)$	$2rg$
$h(=AbaB)$	$2(r^2h+g)$	$2rh$
Total heterozygotes	$2(r^2+1)(g+h)$	$2r(g+h)$
$i(=ABAb)$	$2(r+1)^2i+2r(g+h)$	$2(r+1)i+g+h$
$j(=ABaB)$	$2(r+1)^2j+2r(g+h)$	$2(r+1)j+g+h$
$k(=abAb)$	$2(r+1)^2k+2r(g+h)$	$2(r+1)k+g+h$
$l(=abaB)$	$2(r+1)^2l+2r(g+h)$	$2(r+1)l+g+h$
Total mixed	$2(r+1)^2(i+j+k+l)+8r(g+h)$	$2(r+1)(i+j+k+l)+4(g+h)$
Total	$4(r+1)^2(c+d+e+f+g+h+i+j+k+l)$	$4(r+1)(c+d+e+f+g+h+i+j+k+l)$

Table 31. Self-fertilization. Formulae for the zygotic constitution of the population derived from original parents *ABab* by any number n of successive self-fertilizations.

Let r = the linkage ratio

n = the number of successive self-fertilizations.

$$u = \frac{r}{2(r+1)}$$

$$v = \frac{r^2+1}{2(r+1)^2}$$

$$w = \frac{r^2-1}{2(r+1)^2}$$

The proportions of the 10 diverse classes of zygotes are designated by the letters c to l, as in table 1. Then after n successive generations of self-fertilization:

	Column 1. Linkage = r in both sets of gametes	Column 2. Linkage complete in one of the sets of gametes
Total homozygotes	$\frac{2^{n-1}+1}{2^{n-1}} + v^n$	$\frac{2^{n-1}-1}{2^{n-1}} + u^n$
$c(=ABAB)$	$\frac{2^{n-1}-1}{2^{n+1}} + \frac{v^n+w^n+w^{n-1}+w^{n-2}+\ldots w}{4}$	$\frac{2^{n-1}-1}{2^{n+1}} + \frac{u^n}{2} + \frac{u^{n-1}+u^{n-2}+\ldots u}{4}$
$d(=AbAb)$	$\frac{2^{n-1}-1}{2^{n+1}} + \frac{v^n-w^n-w^{n-1}-w^{n-2}-\ldots w}{4}$	$\frac{2^{n-1}-1}{2^{n+1}} - \frac{u^{n-1}+u^{n-2}+\ldots u}{4}$
$e(=aBaB)$	$=d$	$=d$
$f(=abab)$	$=c$	$=c$
Total heterozygotes	v^n	u^n
$g(=ABab)$	$\frac{v^n+w^n}{2}$	u^n
$h(=AbaB)$	$\frac{v^n-w^n}{2}$	0
Total mixed	$\frac{1}{2^{n-1}} - 2v^n$	$\frac{1}{2^{n-1}} - 2u^n$
$i(=ABAb)$	$\frac{1}{2^{n+1}} - \frac{v^n}{2}$	$\frac{1}{2^{n+1}} - \frac{u^n}{2}$
$j=k=l=i$		

If the original parents are *AbaB:*

The values for c and d are to be interchanged.

" " " e " f " " " "

" " " g " h " " " "

The values for the mixed (i, j, k, l) remain unchanged, also the values for total homozygotes; total heterozygotes; and total mixed.

SOME INTER- AND BACK-CROSSES OF F_1 OENOTHERA HYBRIDS[1]

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In a former paper (DAVIS 1914), I presented data on a number of F_1 hybrids between species crosses of Oenothera chiefly with reference to the studies of Professor DE VRIES on the remarkable crosses between *Oe. biennis* and *Oe. muricata*, where for certain vegetative characters patroclinous tendencies are strongly exhibited. DE VRIES expressed the results in the F_1 generations, for the characters concerned, by the formulae $m \times b = b$ and $b \times m = m$.

It will be remembered that DE VRIES (1911, 1913) has given his conclusions respecting the inheritance of habit and foliage in the inter- and back-crosses by a number of formulae which for *biennis* and *muricata* read as follows:

		Simplified
Double reciprocal	$(b \times m) \times (m \times b) = b$	$m \times b = b$
" "	$(m \times b) \times (b \times m) = m$	$b \times m = m$
Sesquireciprocal	$b \times (m \times b) = b$	$b \times b = b$
"	$(b \times m) \times b = b$	$m \times b = b$
"	$m \times (b \times m) = m$	$m \times m = m$
"	$(m \times b) \times m = m$	$b \times m = m$
Iterative	$b \times (b \times m) = m$	$b \times m = m$
"	$(b \times m) \times m = m$	$m \times m = m$
"	$m \times (m \times b) = b$	$m \times b = b$
"	$(m \times b) \times b = b$	$b \times b = b$

By reducing the expressions which stand for the F_1 hybrids in accordance with the statement that $m \times b = b$ and $b \times m = m$ there is obtained the simplified formulae placed in the second column. The striking feature of the situation is the conclusion of DE VRIES that the pollen involved in all of these combinations makes the same impression whether it is from the species or from an F_1 hybrid and the impression is always in large measure a patroclinous dominance as to features of habit and foliage.

The dominance of the pollen parent expressed in the F_1 hybrids while at times conspicuous is, nevertheless, not an absolute dominance, but is relative in degree, as was shown by the analysis of the F_1 hybrids de-

scribed in my former paper (DAVIS 1914). I was unable to find evidence that a morphological character of either species in the crosses studied was ever passed on to the F_1 hybrids exactly as represented in either of the parents. When the resemblance to one of the parents has been strongest there has always been some trace of the influence of the other species. I was not convinced that the exact duplication of a parental character was ever attained in the F_1 hybrids of the material under consideration, which included crosses between *biennis* and *muricata, biennis* and *Franciscana, biennis* and *grandiflora,* and between *muricata* and *gigas.*

The present contribution will describe some inter- and back-crosses involving the F_1 generations of the species crosses listed above. Unfortunately the cultures were grown a year or two before the methods of experimental germination had been devised which make it possible to obtain complete germination of Oenothera seeds (DE VRIES 1915, DAVIS 1915). Consequently the results here presented can make no claim to complete information on the possibilities of the crosses involved. The percentages of germination from the earth-sown seeds were in certain cases strikingly small and I have since been able to establish from experimental germinations in Petri dishes the degrees of seed fertility that are inherently possible. This data is here included in comparison with the percentages of germination actually obtained from seed in the earth. Information on the facts of seed germination are essential to final conclusions in genetical work on hybrids where the amount of seed sterility is as great as in this material of Oenothera.

Especially necessary is this information on the crosses between *biennis* and *muricata* since these hybrids present an extraordinary amount of seed sterility together with much delayed germination. Consequently, earth-sown cultures of these hybrids frequently very imperfectly give the possibilities of the sowing as to numbers of individuals and we do not know how representative may have been the types obtained. Therefore, the results of my studies have no value as expressions of numbers and ratios and it is more than doubtful whether all of the types or classes represented by viable seeds actually materialized in the cultures. This criticism applies with equal force to the data presented by Professor DE VRIES. I have, however, no hesitation in giving my results, imperfect as they are, since I can at least indicate in certain measure the degree of imperfection, and the data as they stand have direct bearing on the studies of DE VRIES.

HYBRIDS INVOLVING *OENOTHERA BIENNIS* L. AND *OE. MURICATA* L.

(a) Double reciprocal (*biennis* × *muricata*) × (*muricata* × *biennis*), cultures 14.43*a* and 14.43*e*

The seeds of this cross were obtained by pollinating 2 plants of culture 13.33 (F_1, *biennis* × *muricata*, DAVIS 1914, p. 176, figs. 11, 13, 15) from plants of culture 13.34 (F_1, *muricata* × *biennis*, DAVIS 1914, p. 176, figs. 10, 12, 14). The harvest was exceedingly small, as DE VRIES has also reported, very few seeds being developed and these only in the lower portions of the capsules. The seeds, however, were large and many were twice as long as broad. Plants 13.33*a* and 13.33*e* gave respectively 21 seeds from 4 capsules and 52 seeds from 7 capsules.

The germination of the seeds sown in earth, pans kept for 9 weeks,

FIGURE 1.—Double reciprocal (*biennis* × *muricata*) × (*muricata* × *biennis*). Type 2, *muricata*-like in habit, foliage, inflorescence, and buds. Self-sterile.

was extraordinarily poor. From the 21 seeds of plant 13.33*a* only 2 seedlings appeared, culture 14.43*a*, and the 52 seeds of plant 13.33*e* gave only 6 seedlings, culture 14.43*e*. The seedlings all reached maturity, a total of 8 plants from 73 seeds.

According to DE VRIES's formula, $(b \times m) \times (m \times b) = b$, all of the 8 plants should have been similar and *biennis*-like in habit and foliage, but, to my surprise, each of the two cultures presented two types sharply distinguished, which happened to be distributed in equal numbers (culture 14.43*a* 1 + 1, culture 14.43*e* 3 + 3). The points of contrast were not noted until maturity, since as rosettes the plants were similar and *biennis*-like. The striking differences between the two types are tabulated below and comparison may readily be made with a similarly arranged statement of the characters of *biennis* and *muricata* (DAVIS 1914, p. 174).

Double reciprocals (*biennis* × *muricata*) × (*muricata* × *biennis*)

Type 1, *biennis*-like but less vigorous.	Type 2, in important respects *muricata*-like.
Mature plants. About 0.7 m high, similar to *biennis* in habit, but smaller, less vigorous and with fewer branches. Papillae on stem green as in *biennis*.	Mature plants. About 1.2 m high, habit of *muricata* but more branched and stocky, exceptional vegetative vigor (fig. 1). Papillae on stem red as in *muricata*.
Foliage. Leaves resembling those of *biennis* in form and color but generally smaller.	Foliage. Leaves toothed and keeled as in *muricata* but broader (figs. 1 and 2), color a somewhat darker green.
Inflorescence. Bracts ¼ — ½ length of mature buds, in form similar to *biennis* (fig. 3, 14.43*eg*). Younger buds projecting beyond the bracts as in *biennis*.	Inflorescence. Bracts ⅔—¾ length of mature buds, in form similar to *muricata* (fig. 3, 14.43*er*). Bracts projecting beyond the younger buds (fig. 2) as in *muricata*.
Mature buds. About 5 cm long, *biennis*-like in form, in the cone being scarcely angled, in the slender, spreading sepal tips, and in pubescence. (See Fig. 3, 14.43*eg*.)	Mature buds. About 6 cm long, larger than *muricata* but similar in form, in stout cone strongly 4-angled, and in thick appressed sepal tips. (See fig. 3, 14.43*er*.) Pubescence very heavy.
Petals. 1.4 cm long, smaller than those of *biennis* (2—2.3 cm).	Petals. 1.4 cm long, somewhat larger than those of *muricata* (1—1.3 cm).

Stigma lobes. 5 mm long, about 3 mm below tips of anthers, similar to *biennis*.	Stigma lobes. 7 mm long, about 3 mm below tips of anthers, much longer and lower than in *muricata*.
Ovaries. Papillae green.	Ovaries. Papillae red.
Capsules. 2.3—2.5 cm long, similar to those of *biennis*. Self fertile, giving a large yield of seeds.	Capsules. Self sterile, 40 operations to self-pollinate all failures, occasional small capsules developed from open pollinations.
Pollen. 3-lobed and about 50% shriveled as in *biennis*.	Pollen. Perhaps 90% shriveled, the various-sized grains mostly 4-6 lobed.

In view of the conclusions of DE VRIES it is very interesting that my cultures of this double reciprocal should have given two types so distinct as those just described. DE VRIES (1913, pp. 89, 90) reports on a culture of 25 plants all similar and *biennis*-like as in my type 1; he did not obtain type 2 with its resemblance in many points of morphology to *muricata*. It may therefore be questioned whether DE VRIES is correct

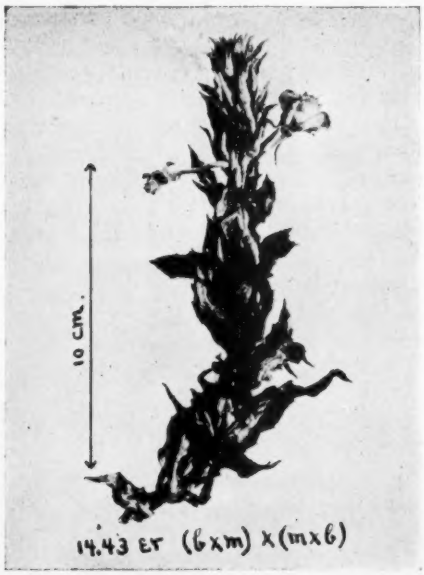

FIGURE 2.—Inflorescence of double reciprocal, type 2, (*biennis* × *muricata*) × (*muricata* × *biennis*), shown in fig. 1, *muricata*-like in foliage, bracts and buds.

in concluding for this double reciprocal that the characters of the *muricata* species are wholly set aside.

As previously stated, from the total of 73 seed-like structures sown in the earth only 8 seedlings appeared after 9 weeks, a germination of 11 percent. I had no seeds remaining to test experimentally the ratio of viable seeds when germination is forced to completion, but judging from my results in other crosses involving *biennis* and *muricata* the percentage of viable seeds should be much greater. It will become a matter of interest, when this cross is repeated and the seeds forced to complete germination, to see whether other types besides the two here reported may be found and a greater degree of segregation established. Since there is in the parent reciprocals, $b \times m$ and $m \times b$, a marked loss of vigor over the parents, *biennis* and *muricata*, and an unusually high degree of pollen sterility, and in the double reciprocal an exceptionally low yield of seeds there would seem to be the probability that large numbers of zygotic combinations are eliminated through the extraordinary mor-

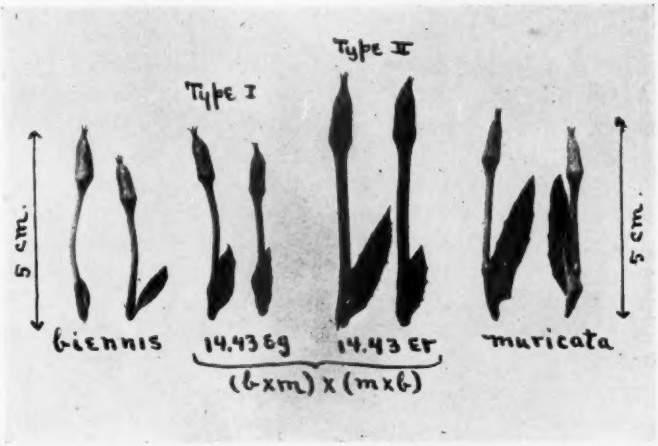

FIGURE 3.—Comparison of the buds and bracts of the two types of double reciprocals (*biennis* × *muricata*) × (*muricata* × *biennis*). Type 1 similar to *biennis*. Type 2 resembling *muricata*.

tality of gametes and zygotes. It is along these lines that the peculiarities of this double reciprocal seem to me more likely to be understood rather than by the hypothesis put forward by DE VRIES.

I selfed a plant of type 1 (14.43*eg*), the *biennis*-like segregate, and the following year obtained 38 seedlings from 304 seeds sown in the

earth, pans kept for 9 weeks, a germination of 12 percent. A subsequent experimental test in Petri dish of 477 seeds from the same harvest showed that 89 percent were actually viable. The 38 seedlings gave a culture, 15.43*g*, of 36 plants, 35 of which were *biennis*-like as DE VRIES described while 1 developed into a narrow-leaved weak type which failed to flower.

The 4 plants representative of type 2 were very interesting on account of their great vegetative vigor as well as for the numerous characters suggestive of *muricata*, and their complete self-sterility was surprising. The facts of this vigor together with the great amount of shriveled pollen (about 90 percent), most of which consisted of 4—6-lobed grains instead of the usual 3-lobed form suggest that the plants had some unusual chromosome complex which failed to behave properly at the time of reduction, after the manner characteristic of triploid forms of Oenothera.

(b) Double reciprocal, (*muricata* × *biennis*) × (*biennis* × *muricata*)

I have twice been prevented from making this cross by the fact that in my garden the plants of the reciprocal *biennis* × *muricata* produced pollen for so short a time that they became completely sterile before the cultures of *muricata* × *biennis* had come to flower and were ready for a cross-pollination. In 1913 the reciprocal *biennis* × *muricata* was represented by 92 plants (culture 13.33), as described in my earlier paper (DAVIS 1914, pp. 176-188). The culture came to flower towards the last of June, producing then less than ½ as much pollen as might be expected from the size of the anthers. By the middle of July pollen was no longer shed, the anthers drying up to small shriveled structures.

Hoping to increase the output of pollen and to lengthen the time of its production I grew in 1914 the same reciprocal, dividing the plants into three groups and heavily treating each with a different type of fertilizer sold by Baugh and Sons Company. The fertilizers used, about 1 kilogram to the square meter, were (1) Baugh's raw bone meal, phosphoric acid 21.5%, ammonia 4.5%, (2) Baugh's balanced plant food, phosphoric acid 10.5%, ammonia 2%, potash 7%, (3) Baugh's high grade potato grower, phosphoric acid 8%, ammonia 4%, potash 10%. Although I obtained somewhat larger plants by this treatment there was apparently no improvement in the amount of pollen formed.

The reverse reciprocal, *muricata* × *biennis*, also exhibited a similar but not quite so high a degree of pollen sterility and treatment with the same fertilizers in 1914 also failed to improve materially the output of pollen.

(c) Sesquireciprocal, *biennis* × (*muricata* × *biennis*)

I was unable to make this cross successfully, taking the pollen from culture 14.34 (*muricata* × *biennis*); 15 attempts during the middle of July gave no seed.

(d) Sesquireciprocal, (*biennis* × *muricata*) × *biennis*, culture 15.31

Pollination of plants in culture 14.33 (*biennis* × *muricata*) from *biennis* resulted in a fair harvest. Sowings in earth of 267 seeds from 7 capsules gave after 9 weeks a culture consisting of 25 seedlings, a germination of 9 percent. A record of complete germination in Petri dish presented 132 seedlings from a sowing of 282 seed-like structures,

FIGURE 4.—A contrast of sesquireciprocals (*biennis* × *muricata*) × *biennis*, culture 15.31, and (*muricata* × *biennis*) × *muricata*, culture 15.35, the former similar to *biennis* (15.16 above), the latter similar to *muricata* (15.20 above).

germination 46 percent. The 25 seedlings grew into mature plants uniform throughout all stages of development and at all times *biennis*-like although with apparently a somewhat greater vigor. A comparison in fig. 4 of the rosette 15.16 with 15.31 will show how close is the resemblance of the hybrid to *biennis*. These observations are in accord with the results of DE VRIES, but since the germination in the earth was so poor the cross should be repeated and cultures grown from seed forced experimentally to a complete expression of seed viability.

(e) Sesquireciprocal, *muricata* × (*biennis* × *muricata*)

The fact that pollen formation in the F_1 hybrid, *biennis* × *muricata* (culture 14.33), ceased after the middle of July, made it impossible to accomplish this cross, since *muricata* in my garden comes to flower later in the summer.

(f) Sesquireciprocal, (*muricata* × *biennis*) × *muricata*, culture 15.35

There were sown in the earth 246 seeds from 5 capsules, which after 9 weeks gave 43 seedlings (culture 15.35), a germination of 17 percent. An experimental test of seed germination forced to completion resulted after 7 weeks in 198 seedlings from about 498 seed-like structures, germination about 40 percent. After the 43 green plants had been potted there began to appear in these pots seedlings with white cotyledons which promptly died; 23 of these were recorded before the green plants were set out in the garden. Since it is my habit to pot cultures in soil seed-sterile, and since these etiolated seedlings or other forms appeared in none of my other cultures I am forced to conclude that they represented a class derived from seeds carried over during the potting of the green plants and therefore the result of delayed germination. Such classes of etiolated seedlings are in my experience not uncommon from hybrids of Oenothera.

Of the green plants, 42 came to maturity and were in all points of morphology similar to *muricata*, but more vigorous, larger-leaved, and more fertile, producing capsules in abundance. The resemblance of the young rosettes to those of *muricata* is shown in fig. 4 (compare 15.35 with 15.20). Thus my observations on the green plants from incomplete germination conforms entirely to DE VRIES's conclusion that $(m \times b) \times m = m$, but I believe that a culture grown from seed experimentally forced to a complete germination would show at least a class of etiolated seedlings with the possibilities of other types.

(g) Iterative, *biennis* × (*biennis* × *muricata*), culture 15.32

The small amount of pollen produced by the F_1, *biennis* × *muricata*, made it difficult to obtain seed of this cross; 12 attempts at pollination gave 2 capsules with a total of 22 seeds. From the 22 seeds sown in earth only 1 seedling appeared after 9 weeks, a germination of 4.5 percent. The single seedling developed into a fine plant *muricata*-like in all points of morphology, but larger-leaved, more vigorous and highly fertile in its seed production. DE VRIES (1913, p. 95) obtained with very much larger cultures plants similar to the F_1 *biennis* × *muricata* but he gives no data on the seed fertility following the cross *b* × (*b* × *m*). My difficulty in obtaining seed together with the low germination in earth leads me to believe, either that all of the classes of viable seeds have not yet been germinated, or that lethal factors eliminate classes of gametes and zygotes.

(h) Iterative, (*biennis* × *muricata*) × *muricata*, culture 15.33

From 212 seeds, contents of 6 capsules, sown in the earth, I obtained after 9 weeks only 2 seedlings, a germination of 0.9 percent. A test in a Petri dish of 292 seeds from the same harvest gave after 7 weeks a complete germination of 42 seeds or 14 percent. One of the seedlings developed into a vigorous, highly fertile plant, *muricata*-like in morphology but larger-leaved; the other plant was dwarfed and weak, failing to flower, but with foliage similar to *muricata*. DE VRIES (1913, p. 96), who was fortunate in having very much larger cultures, reports that the plants without exception were of the type of the F_1, *biennis* × *muricata*. The obvious habit of delayed germination will make necessary further studies of this cross from seeds forced to complete germination, and the low percentage of viable seeds emphasizes the problems of gametic and zygotic sterility which run through so much of the work on Oenothera genetics.

(i) Iterative, *muricata* × (*muricata* × *biennis*), culture 15.36

A sowing of 198 seeds from 6 capsules gave after 9 weeks in earth 51 seedlings, germination 25.7 percent. By the time the rosettes were ¼ grown it was evident that their characters were intermediate between those of the parents (in fig. 5 compare 15.36 with 15.16 and 15.20), and similar to the rosettes of the F_1 hybrid *muricata* × *biennis* (see DAVIS 1914, fig. 2, *muricata* × *biennis*). The 51 seedlings produced mature plants uniform in appearance and also similar to the F_1 *muricata* × *biennis*.

It will be remembered from my earlier paper (DAVIS 1914, pp. 176-181, figs. 10, 12, 14, 15) that this hybrid, *muricata* × *biennis*, was patroclinous only in so far that the foliage of the rosettes and mature plants resembled more strongly that of the pollen parent, but that this resemblance was very far from a duplication of the characters of *biennis* since the leaves were intermediate in form and size. This hybrid was markedly matroclinous in the length of the bracts relative to the length of the buds and in the form of the sepal tips. Now the iterative hybrids presented these same characters to so similar a degree that the formula $m \times (m \times b) = (m \times b)$ expresses very accurately the facts, and like the cross $m \times b$ the iteratives were highly sterile. My results are apparently in full accord with those of DE VRIES but I should emphasize the fact that none of the characters of either parent were represented in pure form in the hybrids. The relatively low seed fertility and exceedingly high degree of pollen sterility strongly suggest that the hybrids may be representative of the only class able to survive in fair numbers the conditions of high mortality among the gametes and zygotes.

(j) Iterative, (*muricata* × *biennis*) × *biennis*, culture 15.34

These hybrids were of exceptional interest since they presented the same characters as the iterative *muricata* × (*muricata* × *biennis*) just described. From 217 seeds sown in earth, contents of 4 capsules, 47 seedlings were obtained after 9 weeks, a germination of 21.6 percent. From the fact that a sowing of about 373 seeds in a Petri dish gave after 4 weeks 73 seedlings, a germination of 19.5 percent, it would seem as though the germination in the earth must have been essentially complete. The ¼-grown rosettes were intermediate between the parents (in fig. 5 compare 15.34 with 15.16 and 15.20), indistinguishable from the rosettes of the iterative $m \times (m \times b)$ (in fig. 5, compare 15.34 with 15.36), and also similar to the F_1 hybrid $m \times b$ (see DAVIS 1914, fig. 2, *muricata* × *biennis*). All of the 47 seedlings developed into mature plants, uniform and of the same type as the iterative $m \times (m \times b)$ and the F_1 $m \times b$; they were likewise highly sterile. Thus my results with this iterative cross were the same as those of DE VRIES, but again the low seed fertility and high pollen sterility present factors that cannot be disregarded in an interpretation of the conclusions and lead me to believe that the plants so far grown are representative of only one class of hybrids, and that through the sterile and abortive seeds and by the pollen degeneration are eliminated other types of which we have no information.

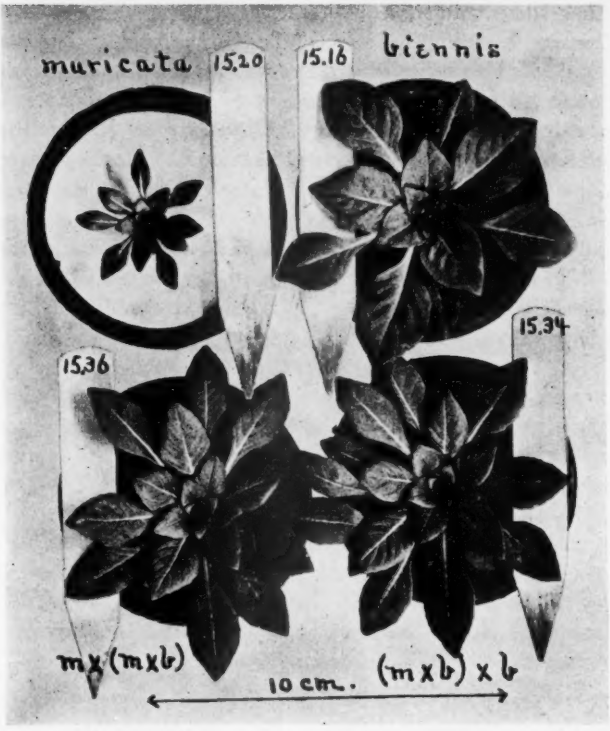

FIGURE 5.—Comparison of the iteratives *muricata* × (*muricata* × *biennis*), culture 15.36, and (*muricata* × *biennis*) × *biennis*, culture 15.34. These iteratives are essentially indistinguishable from one another and similar to the F_1 hybrid *muricata* × *biennis*. They present rosette characters intermediate between those of the parents, *biennis* (15.16) and *muricata* (15.20) shown above.

(k) Remarks

I do not wish at this time to discuss the interesting theory of DE VRIES for the reported behavior of *biennis* and *muricata* in the inter- and back-crosses and also in the F_2 generations, since I am confident that we have not as yet the full data before us. My success in obtaining 2 types of plants from the double reciprocal $(b \times m) \times (m \times b)$ where DE VRIES found only 1 and in finding a class of etiolated seedlings in the sesquireciprocal $(m \times b) \times m$ leads me to believe that cultures grown from seed forced to complete germination may show a greater variety

of forms. I also obtained in the iteratives $b \times (b \times m)$ and $(b \times m) \times m$ plants with the morphology of the *muricata* parent but even more vigorous and highly fertile while DE VRIES reports plants of the type of the F_1, *biennis* × *muricata*. The extent of delayed germination among these hybrids is undoubtedly very great and only by methods of experimental germination which preserve the residue of sterile structures for examination can we be certain that cultures exhibit the full possibilities of viable seeds. In table 1 there is given the data on seed germination in my cultures of hybrids involving *biennis* and *muricata* and a glance will show how low was the percentage of germination obtained from sowings in earth even though the seed pans were for the most part kept as long as 9 weeks. Of especial interest are the comparisons that may be made of 5 records of earth-sown cultures with experimental germinations from the same harvests in Petri dishes; 15.43*g* with *15.43*g*, 15.31 with *15.31, 15.35 with *15.35, 15.33 with *15.33, and 15.34 with *15.34. These records show generally that the sowings in earth brought forth only a small fraction of the viable seed.

TABLE 1

Seed germination in crosses involving *Oenothera biennis* and *Oe. muricata*

Culture	Cross	Seeds sown	Sown in	Seedlings	Percent of germination	Duration of experiment
14.43	Double reciprocal, $(b\times m)\times(m\times b)$	73	Earth	8	11.0	9 weeks
15.43*g*	F_2, Double reciprocal, 14.43*eg* selfed	403	Earth	38	12.0	9 weeks
*15.43*g*	F_2, Double reciprocal, 14.43*eg* selfed	477	Petri dish	427	89.0	6 weeks
15.31	Sesquireciprocal, $(b\times m)\times b$	267	Earth	25	9.0	9 weeks
*15.31	Sesquireciprocal, $(b\times m)\times b$	282	Petri dish	132	46.0	6 weeks
15.35	Sesquireciprocal, $(m\times b)\times m$	246	Earth	43	17.0	9 weeks
*15.35	Sesquireciprocal, $(m\times b)\times m$	498	Petri dish	198	40.0	7 weeks
15.32	Iterative, $b\times(b\times m)$	22	Earth	1	4.5	9 weeks
15.33	Iterative, $(b\times m)\times m$	212	Earth	2	0.9	9 weeks
*15.33	Iterative, $(b\times m)\times m$	292	Petri dish	42	14.0	7 weeks
15.36	Iterative, $m\times(m\times b)$	198	Earth	51	25.7	9 weeks
15.34	Iterative, $(m\times b)\times b$	217	Earth	47	21.6	9 weeks
*15.34	Iterative, $(m\times b)\times b$	373	Petri dish	73	19.5	4 weeks
14.41	F_2, *biennis* × *muricata*	466	Earth	8	1.7	9 weeks
14.42	F_2, *muricata* × *biennis*	205	Earth	35	12.0	9 weeks
13.33	F_1, *biennis* × *muricata*	673	Earth	139	20.0	6 weeks
13.34	F_1, *muricata* × *biennis*	153	Earth	97	63.0	7 weeks

Delayed germination is, however, only one of the factors in the genetical problems of fertility presented by these interesting crosses. There was an immense amount of seed sterility presented in the records *15.31, *15.35, *15.33, and *15.34, as proved by the residue of seeds empty of contents and by numerous abortive structures of smaller size. Also, there is the wide-spread pollen degeneration which gives to these hybrids usually a remarkably small output of pollen, and possibly correlated with this is the large amount of ovule powder representing ovules which either were not fertilized or if fertilized failed to develop further. Until this data on gametic and zygotic sterility is assembled and understood in its cytological and physiological bearings we are in no position to hold more than tentative hypotheses. I am inclined to believe that the relatively few types so far described among these hybrids represent a limited number of classes able to survive the very extensive mortality among the gametes and zygotes. The number of classes is, I think, likely to be materially increased through cultures grown from seed forced experimentally to complete germination.

The interesting facts so far before us show that many of the characters of *biennis* and *muricata* are inherited in close correlation or, in other words, are closely linked, and this principle seems generally to be established by studies on Oenothera genetics. With respect to the crosses under consideration the combined results of DE VRIES and myself may be summarized as follows:

		DE VRIES	DAVIS
Double reciprocal	$(b\times m)\times(m\times b)=$	*biennis*	*biennis* (4 plants), and a sterile form somewhat *muricata*-like (4 plants)
Double reciprocal	$(m\times b)\times(b\times m)=$	*muricata*	No data
Sesquireciprocal	$b\times(m\times b)=$	*biennis*	No data
Sesquireciprocal	$(b\times m)\times b=$	*biennis*	*biennis* (25 plants)
Sesquireciprocal	$m\times(b\times m)=$	*muricata*	No data
Sesquireciprocal	$(m\times b)\times m=$	*muricata*	*muricata* (43 plants), and a class of etiolated seedlings (23 plants)
Iterative	$b\times(b\times m)=$	*biennis*×*muricata*	*muricata* (1 plant)
Iterative	$(b\times m)\times m=$	*biennis*×*muricata*	*muricata* (2 plants)
Iterative	$m\times(m\times b)=$	*muricata*×*biennis*	*muricata*×*biennis* (51 plants)
Iterative	$(m\times b)\times b=$	*muricata*×*biennis*	*muricata*×*biennis* (47 plants)

The points of difference in the conclusions as tabulated above indicate to me that further studies are likely to increase the number of types

which will be obtained from these crosses when cultures have been grown in which we may feel certain that all of the seeds have germinated. The results so far indicate that the characters of the hybrids for the most part, as represented in the viable seeds, are similar to one or the other of the parents or similar to the F_1 hybrids. If the characters should prove to be correlated with little variation from so simple an arrangement the different types of viable gametes formed would be relatively few in number, and the data on sterility both gametic and zygotic may give, when assembled, the key to the peculiarities of these interesting hybrids.

HYBRIDS INVOLVING *OENOTHERA BIENNIS* L. AND *OE. FRANCISCANA* BARTLETT

My studies on hybrids between *Oenothera biennis* and *Oe. Franciscana* have had for me the greatest interest with respect to the evidence for the segregation of parental characters shown in the F_2 generation (DAVIS 1916), and with reference to the *Lamarckiana*-like forms that may be found among these segregates. I have, however, grown a full set of double reciprocals, sesquireciprocals and iterative hybrids from crosses with the race *Franciscana* E. The characters of *Franciscana* will be found contrasted with those of *biennis* in the paper on the F_2 generations of that cross (DAVIS 1916, pp. 206, 207), and the characters of the F_1 reciprocal hybrids are compared in the earlier paper (DAVIS 1914, pp. 190, 191). I shall now only report briefly the chief features of the back- and inter-crosses, following the order of descriptions as just given in the account of the same crosses between *biennis* and *muricata*. It will be noted that the results do not follow consistently the formulae given by DE VRIES for the inter- and back-crosses of the F_1 reciprocals of *biennis* and *muricata;* compare p. 156 with p. 175.

(a) Double reciprocal, (*biennis* × *Franciscana* E) × (*Franciscana* E × *biennis*), culture 15.62

A sowing of 302 seeds, contents of 2 capsules, in earth, gave after 9 weeks 72 seedlings, germination 23.8 percent. A test of seed viability in a Petri dish produced 342 seedlings from about 657 seed-like structures with an additional residue of 130 abortive seeds, germination 52 percent. Shoots were developed from 51 rosettes, 11 of which were *biennis*-like, the others mostly resembling *Franciscana* or having characters intermediate between the parents; there was an eventual mortality of 21 plants mostly from a group of dwarfs. The stems all had the red papillae of *Franciscana*. The foliage on shoots from the *biennis*-

like rosettes was similar to *biennis* and the buds, flowers and capsules were also like those of *biennis*. The *Franciscana*-like rosettes produced plants with foliage and buds of this parent but fully half of the plants had flowers of the size and form of *biennis*. The culture thus, failing to hold to one type, clearly differentiated several classes of hybrids. The low germination of the earth-sown culture does not justify further discussion.

(b) Double reciprocal, (*Franciscana* E × *biennis*) × (*biennis* × *Franciscana* E), culture 15.61

The seed germination of this cross in the earth was 30 percent, and that of an experimental test 34 percent, so there is some reason for regarding the culture as fairly representative. There appeared at the end of 8½ weeks 73 seedlings from a sowing of 243 seeds, contents of 2 capsules. Of the 63 rosettes which survived 3 were *biennis*-like, 15 intermediate, 38 *Franciscana*-like and the others were narrow-leaved dwarfish types. Shoots were sent up from 63 rosettes and all were red papillate as in *Franciscana*. One of the *biennis*-like rosettes produced a plant with foliage, buds and capsules of this parent but with a petal size and stigma relation of *Franciscana;* the other two rosettes developed into plants which resembled *Franciscana* in foliage, buds and capsules but had the smaller petals and shorter style of *biennis*. The *Franciscana*-like rosettes and those intermediate all developed shoots similar to *Franciscana* in foliage and buds but with flower size and structure *biennis*-like in 33 of the 53 plants. The culture at maturity with the exception of 1 plant consisted then of types *Franciscana*-like as to foliage, bud form and capsules, but with a wide range of flowers from a size and structure as in *biennis* to flowers indistinguishable from those of *Franciscana*. The segregation was remarkably clear-cut in 17 plants which were very close to the *Franciscana* parent, but as a whole the culture was far from uniform.

(c) Sesquireciprocal, *biennis* × (*Franciscana* E × *biennis*), culture 15.64

This cross proved to be of exceptional interest for its well defined segregates and especially for the appearance of green-stemmed plants in contrast to those with red papillae. A sowing in earth of 151 large seeds from 1 capsule produced after 8½ weeks 27 seedlings, a germination of about 18 percent. Experimental germination of 432 seeds gave 323 seedlings, about 75 percent, so that the earth-sown culture was

very far from representative of the seed viability. Of the rosettes, 11 were *biennis*-like, 11 intermediate, 1 *Franciscana*-like and 4 were narrow-leaved dwarfs. The shoots from the *biennis*-like rosettes were green (papillae not red) and all of these plants were also *biennis*-like in foliage, buds, flowers and capsules; they constituted a remarkable class of segregates in all respects similar to the *biennis* parent. The rosettes intermediate in character or *Franciscana*-like developed shoots with red papillae and likewise presented foliage and buds as in *Franciscana,* but all had the smaller petals and shorter styles of *biennis.* Thus about ½ of the plants were like the *biennis* parent, while *Franciscana* characters of stem coloration, foliage and buds, appeared in the remainder of the culture.

(d) Sesquireciprocal, (*biennis*×*Franciscana* E)×*biennis,* culture 15.67

This cross gave a progeny remarkably uniform and possibly fairly representative of the viable seeds. The earth-sown culture consisting of 159 seeds from 1 capsule gave after 12 weeks 46 seedlings, germination about 29 percent; in a Petri dish 593 seeds produced 193 seedlings, germination 32.5 percent. As rosettes 44 of the plants were *biennis*-like and 2 were narrow-leaved dwarfs which died; 40 plants of the *biennis*-like group came to maturity. They were strong plants similar to *biennis* in habit, foliage, bud and flower structure, but with longer capsules (2.5-3 cm) and all with the red papillae of *Francicsana.* Thus the color peculiarity of *biennis* (green stems) together with the short capsules failed to segregate with the other conspicuous characters of this parent species.

(e) Sesquireciprocal, *Franciscana* E × (*biennis* × *Franciscana* E), culture 15.70

This cross was represented by a relatively large number of plants; 248 seeds, from 1 capsule, gave in the earth after 8½ weeks 124 seedlings, germination 50 percent. A test in Petri dish of 603 seed-like structures resulted in 533 seedlings, germination 88 percent. The culture matured 90 plants and was uniformly *Franciscana*-like in the form of the rosette, in having red papillae over the stems in the form of the foliage, bud tips and capsules. There was a wide range of flower size, most of the plants approaching *biennis* in having smaller petals and a lower position of the stigma, and there was likewise much variation in the size of the leaves; 15 plants were *Franciscana*-like in all respects. A group of 22 backward plants remained as dwarf rosettes.

(f) Sesquireciprocal, (*Franciscana* E × *biennis*) × *Franciscana* E, culture 15.65

From 154 large seeds, contents of 1 capsule, sown in the earth there were obtained after 8½ weeks 41 seedlings, a germination of 26 percent; tested in Petri dish 220 seeds gave 100 seedlings, germination 45 percent. The culture matured 37 plants of which 1 was green-stemmed and *biennis*-like in all other respects except for larger capsules and a weak branching. The other 36 plants were uniformly *Franciscana*-like as rosettes, in foliage, buds and in having red papillae. They exhibited, however, many flowers approaching *biennis* in size and position of stigma; 16 plants were in all respects *Franciscana*-like.

(g) Iterative, *biennis* × (*biennis* × *Franciscana* E), culture 15.68

In this cross the germination of 108 seeds in earth, giving 40 seedlings, 37 percent, after 8½ weeks was higher than that of 145 seed-like structures in a Petri dish, 45 seedlings, 31 percent. A high mortality among the rosettes, however, reduced the number of plants that matured to 23. These were all *Franciscana*-like as rosettes, in foliage, buds, and capsules, and in having red papillae. The flower size was generally smaller than that of *Franciscana* and the leaves were frequently larger; 9 plants were quite indistinguishable from *Franciscana*. A single narrow-leaved dwarf was present.

(h) Iterative, (*biennis* × *Franciscana* E) × *Franciscana* E, culture 15.69

This cross furnished another example of an earth-sown culture giving a germination equal to the test in a Petri dish. Sowings of 177 seeds after 8½ weeks resulted in 99 seedlings, germination 56 percent; about 300 seed-like structures in a Petri dish gave 171 seedlings, germination 57 percent. There matured 96 plants all *Franciscana*-like as rosettes, in foliage, in buds, and in having red papillae, but the flower size was generally smaller than that of *Franciscana* and the stigma frequently occupied a somewhat lower position; 11 plants were in all respects *Franciscana*-like. The cross then reproduced essentially the characters exhibited by the iterative *biennis* × (*biennis* × *Franciscana* E), and like the latter consisted of exceptionally vigorous plants frequently larger-leaved than the parent which it so closely resembled in its vegetative characters. Dwarfs were represented by 1 narrow-leaved plant.

(i) Iterative, *Franciscana* E × (*Franciscana* E × *biennis*), culture 15.66

A sowing of 263 seeds from one capsule in earth gave after 8½

weeks 126 seedlings, germination 48 percent; experimentally tested, 741 seeds gave 581 seedlings, germination 78 percent. The presence of 6 etiolated rosettes which died, together with further mortality, reduced the number of plants that matured to 111; of these all agreed in having red papillae on the stems. In other respects the culture presented wide divergence of types; 17 plants had foliage, bud tips and capsules *biennis*-like, and of these, 3 plants bore flowers of the size and form of *biennis*, 7 were intermediate between the parents, and 7 had flowers similar to those of *Franciscana;* 94 plants were *Franciscana*-like in foliage, bud tips and capsules, but of these only 26 had flowers with the size and form of *Franciscana*, 63 presenting flowers intermediate in structure, 4 essentially duplicating the flower type of *biennis* and 1 plant presenting smaller petals (1.4 cm). Thus none of the segregates fully represented *biennis*, since all had red papillae, but 26 were of the *Franciscana* type.

(j) Iterative, (*Franciscana* E × *biennis*) × *biennis*, culture 15.63

This cross resembled *biennis* in all respects except that the stems all bore the red papillae of *Franciscana* and the capsules, uniformly longer, were similar to those of the latter parent. From 206 seeds, contents of 2 capsules, sown in earth 100 seedlings appeared after 8½ weeks, germination 48.5 percent; in a Petri dish 238 seeds gave 188 seedlings, germination 79 percent. Only 45 plants grew to maturity, there being 40 etiolated dwarf rosettes which died and other plants which either remained as rosettes or failed to survive the summer. Of the 45 rosettes which sent up shoots 34 were *biennis*-like and the remainder had larger and more crinkled leaves somewhat as in *Lamarckiana*. The culture at maturity was remarkably uniform and *biennis*-like in foliage, buds, flower size and structure, but as noted above showed the red papillae of *Franciscana* together with *Franciscana*-like capsules (2.7-3 cm long).

(k) Remarks

The surprising feature of the double reciprocals, sesquireciprocals and iterative hybrids involving *biennis* and *Franciscana* E is the much greater variety of segregation exhibited as contrasted with that known for similar hybrids in which *biennis* and *muricata* are concerned. It is impossible to express the facts in simple formulae, but the most striking features are presented below.

Double reciprocal	$(b\times f)\times(f\times b)$	Type I, *biennis*-like except for red papillae (11 plants). Type II, *Franciscana*-like in red papillae, foliage and buds, but various as to flower form and size (40 plants).
	$(f\times b)\times(b\times f)$	Type I, *biennis*-like except for red papillae and large flowers (1 plant). Type II, generally *Franciscana*-like in red papillae, foliage and buds, but various as to flower form and size (62 plants).
Sesquireciprocal	$b\times(f\times b)$	Type I, *biennis*-like in all respects (11 plants). Type II, *Franciscana*-like in red papillae, foliage and buds, but with flowers similar to *biennis* (12 plants).
	$(b\times f)\times b$	*Biennis*-like except for red papillae and longer capsules (40 plants).
	$f\times(b\times f)$	*Franciscana*-like except for wide variation in flower size and form, most of the plants in this respect approaching *biennis* (90 plants).
	$(f\times b)\times f$	Type I, *biennis*-like (1 plant). Type II, *Franciscana*-like in red papillae, foliage and buds, but various as to flower form and size (36 plants).
Iterative	$b\times(b\times f)$	*Franciscana*-like except that flowers were generally smaller (23 plants).
	$(b\times f)\times f$	*Franciscana*-like except that flowers were generally smaller (96 plants).
	$f\times(f\times b)$	Type I, *biennis*-like except for red papillae and flowers various in form and size (17 plants). Type II, *Franciscana*-like in red papillae, foliage, buds, and capsules, but various as to flower form and size (94 plants).
	$(f\times b)\times b$	*Biennis*-like except for red papillae and longer capsules (45 plants). A group of 40 etiolated dwarf rosettes died early.

Comparison of these data with those given for the same crosses between *biennis* and *muricata* (page 169) will show at a glance how much more involved are the facts and how impossible it is to bring the conclusions into line with the simple formulae which DE VRIES offers for the hybrids between *biennis* and *muricata*. Does this more extensive segregation depend upon fundamental differences between the parent types, *Franciscana* and *muricata?* I venture to believe that it probably does not but that the much greater seed sterility of the *biennis-muricata* crosses masks a similar degree of segregation which has not been expressed in the small cultures so far obtained and may never be expressed because

of the extraordinary mortality among the gametes and zygotes of these hybrids.

To bring out clearly the greater degree of fertility in the *biennis-Franciscana* crosses I have prepared a statement, table 2, of my data on seed germination arranged so that it may be readily compared with table 1 which gives my data for the same crosses between *biennis* and *muricata*. It will be easily seen that the germination percentages of the *biennis-Franciscana* crosses are in general very much higher than those for the hybrids involving *biennis* and *muricata*. Thus the double reciprocal $(b\times f)\times(f\times b)$ in earth gave a germination of 23.8 percent while that of $(b\times m)\times(m\times b)$ was 11 percent; the sesquireciprocal $(b\times f)\times b$ 29 percent and $(b\times m)\times b$ 9 percent; the iteratives $b\times(b\times f)$ 37 percent and $b\times(b\times m)$ 4.5 percent; $(b\times f)\times f$ 56 percent and $(b\times m)\times m$ 0.9 percent; $f\times(f\times b)$ 48 percent and $m\times(m\times b)$ 25.7 percent; $(f\times b)\times b$ 48 percent and $(m\times b)\times b$ 21.6 percent.

The table also shows some of the striking gains in percentage when seeds are germinated in Petri dishes; compare 15.62 with *15.62, 15.63 with *15.63, 15.64 with *15.64, 15.65 with *15.65, 15.66 with *15.66 and 15.70 with *15.70. In certain cases the germination in the Petri dishes was not so large as the germination in the earth; compare 15.68 with *15.68, and 15.38 with *15.38. Of especial interest is the comparison of 15.37 with *15.37 and 15.38 with *15.38 for the pans containing the earth-sown seeds were in these cultures kept for 16 months and the last seedlings appeared as late as 13 and 11 months after the sowing while 8½ and 3½ weeks respectively brought a complete germination in the Petri dishes.

In the segregation displayed by the crosses between *biennis* and *Franciscana* the following close correlations of characters were quite as conspicuous as the correlations displayed in the *biennis-muricata* crosses. (1) Plants *biennis*-like in all respects were found in the sesquireciprocals $b\times(f\times b)$ and $(f\times b)\times f$. (2) *Biennis*-like classes, except for red papillae, were present in both double reciprocals, in the sesquireciprocal $(b\times f)\times b$, and in the iteratives $f\times(f\times b)$ and $(f\times b)\times b$. (3) Plants *Franciscana*-like in red papillae, foliage and buds, constituted the entire cultures of the sesquireciprocal $f\times(b\times f)$, and of the iteratives $b\times(b\times f)$ and $(b\times f)\times f$, and appeared as classes in the double reciprocals, the sesquireciprocals $b\times(f\times b)$ and $(f\times b)\times f$, and in the iteratives $f\times(f\times b)$ and $(f\times b)\times b$. In view of the imperfect germination in these earth-sown cultures I do not believe that the data give all

TABLE 2

Seed germination in crosses involving *Oenothera biennis* and *Oe. Franciscana*

Culture	Cross	Seeds sown	Sown in	Seedlings	Percent of germination	Duration of experiment
15.62	Double reciprocal $(b\times f)\times(f\times b)$	302	Earth	72	23.8	9 weeks
*15.62	Double reciprocal $(b\times f)\times(f\times b)$	657	Petri dish	342	52	10 weeks
15.61	Double reciprocal $(f\times b)\times(b\times f)$	243	Earth	73	30	8½ weeks
*15.61	Double reciprocal $(f\times b)\times(b\times f)$	109	Petri dish	39	34	8 weeks
15.64	Sesquireciprocal $b\times(f\times b)$	151	Earth	27	17	8½ weeks
*15.64	Sesquireciprocal $b\times(f\times b)$	432	Petri dish	323	75	7 weeks
15.67	Sesquireciprocal $(b\times f)\times b$	159	Earth	46	29	8½ weeks
*15.67	Sesquireciprocal $(b\times f)\times b$	593	Petri dish	193	32	7 weeks
15.70	Sesquireciprocal $f\times(b\times f)$	248	Earth	124	50	8½ weeks
*15.70	Sesquireciprocal $f\times(b\times f)$	603	Petri dish	533	88	4 weeks
15.65	Sesquireciprocal $(f\times b)\times f$	154	Earth	41	26	8½ weeks
*15.65	Sesquireciprocal $(f\times b)\times f$	220	Petri dish	100	45	10 weeks
15.68	Iterative $b\times(b\times f)$	108	Earth	40	37	8½ weeks
*15.68	Iterative $b\times(b\times f)$	145	Petri dish	45	31	10 weeks
15.69	Iterative $(b\times f)\times f$	177	Earth	99	56	8½ weeks
*15.69	Iterative $(b\times f)\times f$	300	Petri dish	171	57	10 weeks
15.66	Iterative $f\times(f\times b)$	263	Earth	126	48	8½ weeks
*15.66	Iterative $f\times(f\times b)$	741	Petri dish	581	78	10 weeks
15.63	Iterative $(f\times b)\times b$	206	Earth	100	48	8½ weeks
*15.63	Iterative $(f\times b)\times b$	238	Petri dish	188	79	8 weeks
15.37	F_2, *Franciscana* E × *biennis*	396	Earth	195	49	16 months
*15.37	F_2, *Franciscana* E × *biennis*	982	Petri dish	513	52	8 weeks
15.38	F_2, *biennis* × *Franciscana* E	367	Earth	250	68	16 months
*15.38	F_2, *biennis* × *Franciscana* E	562	Petri dish	322	57	3½ weeks
14.51	F_2, *Franciscana* B × *biennis*	819	Earth	402	49	11 weeks
15.51	F_2, *Franciscana* B × *biennis*	921	Petri dish	761	82.6	3½ weeks
15.52	F_2, *biennis* × *Franciscana* B	623	Petri dish	438	70	3½ weeks
15.46	F_1, *Franciscana* E × *biennis*	955	Petri dish	875	91.6	5 weeks
15.47	F_1, *biennis* × *Franciscana* E	510	Petri dish	430	84	9 weeks
13.35	F_1, *Franciscana* B × *biennis*	652	Earth	328	50	4-7 weeks
15.44	F_1, *Franciscana* B × *biennis*	636	Petri dish	606	95	5½ weeks
13.36	F_1, *biennis* × *Franciscana* B	381	Earth	167	43.8	6-7 weeks
15.45	F_1, *biennis* × *Franciscana* B	440	Petri dish	304	69	6 weeks

of the possibilities of the viable seeds, but, such as they are, the records show a remarkable degree of linkage between certain characters.

I have throughout emphasized the fact that the characters of the rosettes, foliage, bud tips, capsules, and stem coloration (papillae either red or green) generally segregate clearly towards one or the other of the parents. There is, however, considerable variation in the size of organs, a variation extremely difficult to classify and probably subject to much fluctuation. Flower structure presented itself in a wide range

of size and relationships of anthers to stigmas, giving much less frequently conditions resembling the parents. Plants with red papillae were much more numerous than green-stemmed plants which were found only in the sesquireciprocals $b \times (f \times b)$ and $(f \times b) \times f$ where these plants in other respects were *biennis*-like. The plants of other crosses, *biennis*-like in all other respects, had red papillae. It is curious that in the sesquireciprocal $b \times (f \times b)$ the green-stemmed plants (11) were almost equal in number to those with red papillae (12), but the germination was only 17 percent in the earth-sown cultures while the tests in the Petri dish showed 75 percent of viable seeds.

HYBRIDS INVOLVING *OENOTHERA BIENNIS* L. AND *OE. GRANDIFLORA* SOLANDER

I am able to report only on the double reciprocals of the crosses between *Oenothera biennis* and *Oe. grandiflora*, the parent reciprocals being plants of the cultures (12.48 and 12.49) described in my paper of 1914, pp. 192-196, where will also be found a description of the race *grandiflora* D. The F_1 reciprocal crosses resembled the pollen parent and were consequently patroclinous (1) in the morphology of the rosettes and in the relative promptness with which the rosettes sent up their central shoots, (2) in the height and branching habit of the mature plants, (3) in the form of the leaves, (4) in the morphology of the inflorescence, (5) in the position of the stigma relative to the anthers, (6) in the time of flowering, (7) in the length of the capsules. Nevertheless, here as in other reciprocal crosses I failed to find certain evidence that any character of the pollen parent appeared in the F_1 hybrids in absolutely unmodified form; a matroclinous tendency was exhibited in the form of the sepal tips.

There will also be given a brief description of cultures in the F_2 from the F_1 plants, 12.48*a*, *grandiflora* D × *biennis*, and 12.49*a*, *biennis* × *grandiflora* D, which were the parents of the double reciprocals. This account is of considerable interest when taken in relation to the low percentage of germination obtained.

(a) Double reciprocal, (*biennis* × *grandiflora* D) × (*grandiflora* D × *biennis*), culture 13.44

From a sowing in earth of 221 seeds, contents of 1 capsule, there appeared after 7½ weeks 98 seedlings, a germination of 44 percent. About ½ of the seedlings presented cotyledons partly or wholly etiolated and from among these a group of 30 weak dwarfs developed with a very short abortive root system and a close cluster of narrow leaves,

FIGURE 6.—A dwarf type from the F_2 of *grandiflora* D × *biennis*, culture 13.41, and represented also in the F_2 of *biennis* × *grandiflora* D, culture 13.42, and in the two double reciprocals, cultures 13.43 and 13.44. Rosettes a close cluster of narrow leaves generally somewhat etiolated and not more than 1—2 cm long, a very short abortive root system.

generally somewhat etiolated and mostly not more than 1-2 cm long (fig. 6). Many of these dwarfs promptly died and none grew sufficiently large to plant in the garden. There were set out 68 plants which as rosettes presented a varied assortment some tending towards the *biennis* and some towards the *grandiflora* parent; about 15 of these were more or less etiolated but later outgrew this peculiarity. As the culture approached maturity 21 plants exhibited a foliage, habit, and bud tips similar to *biennis* but were much taller plants (1.3-1.5 m high). The remaining 47 plants had narrow leaves intermediate between the parents and none so narrow as those of *grandiflora* D. The flowers exhibited a wide range, some being as small as those of *biennis* and with a similar position of the stigma at or below the level of the anther tips, others being large and with the stigma well beyond the anther tips as in *grandiflora* D. No correlations were discovered between the flower size and other features of morphology. The culture, therefore, was very far from uniform and showed abundant evidence of segregation. Its composition could not be expressed by the formula $(b \times g) \times (g \times b) = b$ which would be the analogue of the formula $(b \times m) \times (m \times b) = b$ given by DE VRIES for the same type of double reciprocal involving *biennis* and *muricata*. In the latter cross the percentage of viable seeds is much lower, a fact which suggests that high seed sterility or delayed germination is responsible for the uniform results obtained by DE VRIES.

(b) Double reciprocal, (*grandiflora* D × *biennis*) × (*biennis* × *grandiflora* D), culture 13.43

A sowing of 217 seeds in earth, from 1 capsule, gave after 7½ weeks 104 seedlings, a germination of 47.9 percent. A class of 33 dwarfs appeared with very short narrow leaves (fig. 6) exactly similar to those in the other double reciprocal (culture 13.44) described above; these likewise were too weak to set out in the garden. There were developed 71 vigorous rosettes fairly uniform and intermediate between the parents but resembling *grandiflora* more than *biennis* especially since they showed extensive anthocyan coloration. At maturity the culture contained 19 plants similar in general morphology to *biennis* but with the anthocyan coloration of *grandiflora;* the other 52 plants had narrower leaves, but not so narrow as those of *grandiflora,* and all showed red coloration in spots and patches sometimes covering the greater part of the leaves. As in the other double reciprocal the flowers varied widely but were mostly of the size of *biennis* and with a similar position of the stigma; a few plants had large flowers of a structure similar to that of *grandiflora.*

The culture therefore as a whole was clearly intermediate between the parent species in all of its morphological features but had the anthocyan coloration of *grandiflora.* Such extreme types as were present had the appearance of segregates. Few plants were sufficiently similar to *grandiflora* to justify the expression of their characters whether of foliage, habit or flowers by the formula $(g \times b) \times (b \times g) = g$.

(c) The F_2 generation, *grandiflora* D × *biennis,* culture 13.41

The second generation from plant 12.48*a*, F_1 *grandiflora* D × *biennis,* consisted of 96 plants as the result of a sowing in earth of 459 seeds from 7 capsules, pans kept for 6½-8 weeks, a germination of 20.9 percent. A class of dwarfs (fig. 6) appeared consisting of 22 plants identical with those described for the double reciprocals and these likewise were too weak to live in the garden. There were brought to maturity 74 plants constituting a remarkably uniform assemblage similar to the parent F_1 hybrid type described for culture 12.48 (Davis 1914, 193-195). Except for this class of dwarfs there was therefore little evidence of variation in the culture as represented by this small germination of 20.9 percent. In view of my experience with the F_2 generation of the cross *Franciscana* × *biennis* (Davis 1916), where segregation was conspicuous after complete germination, experimentally induced, of 52 percent, I must believe that the uniformity of the healthy plants in this culture

of *grandiflora* × *biennis* in the F_2 simply means that delayed germination prevented the appearance of more varied types.

(d) The F_2 generation, *biennis* × *grandiflora* D, culture 13.42

The sowing of 672 seeds from 8 capsules, in earth, parent plant 12.49*a* F_1 *biennis* × *grandiflora* D, gave after 6½-8 weeks 59 plants, a germination of 8.7 percent. Of these plants 11 were dwarfs of the type present in the cultures of the double reciprocals, and in the F_2 from *grandiflora* D × *biennis;* they also died early. This left a culture of 48 plants which matured and these were uniform and similar to the parent F_1 hybrid type described for culture 12.49 (DAVIS 1914, pp. 193-195). A seed germination as low as 8.7 percent indicates that the culture must have been very far from representative of the possibilities of the viable seeds and suggests delayed germination as the reason why there was no greater variation in the culture.

(e) Remarks

One of the most interesting features of these crosses involving *biennis* and *grandiflora* D has been the constant appearance of the same characteristic dwarfs in the relatively large proportions of 18.6-31.7 percent of the totals in the cultures. These are large proportions although the figures can have no genetical significance in view of the low and evidently incomplete germinations obtained from these earth-sown seeds. It is perhaps possible that these peculiar dwarfs with their numerous small leaves and abortive roots (fig. 6) are diseased plants, yet their comparatively uniform structure and large numbers would suggest a genetical reason for their presence. There would seem to me to be every probability that cultures of these and other crosses in which *biennis* and *grandiflora* are concerned would show either unmistakable segregation where germination is experimentally forced to completion, or degrees of sterility that would account for missing classes.

HYBRIDS INVOLVING *OENOTHERA MURICATA* L. AND *OE. GIGAS* DE VRIES

These crosses offer some very interesting problems in cytology and sterility upon which I hope later to make a report. Cultures of the F_1 hybrids in my experience (DAVIS 1914, pp. 197-203) have given similar reciprocals as far as the larger plants were concerned, but narrow-leaved forms are frequently present in the cross *muricata* × *gigas,* a fact noted also by DE VRIES (1913, p. 181). The F_1 of *muricata* × *gigas* is not difficult to obtain; germinations in a Petri dish from the contents of 4 capsules (culture 16.30) gave after 5 weeks 11 seedlings and a

residue of 11 large empty seeds, 3 seeds with contents, and a large amount of abortive structures grading into ovule powder. The reciprocal cross *gigas* × *muricata* yielded an extraordinarily small harvest of viable seeds; the contents of 3 capsules (culture 16.29) gave after 5 weeks in a Petri dish 1 seedling and a residue of 230 large empty seed-like structures. The F_1 hybrids have with one culture excepted (DAVIS 1914, p. 197) proved to be self-sterile both in my experience and in that of DE VRIES. I have made in the past 5 years (1912-1916) 237 attempts to self *muricata* × *gigas* and 102 attempts to self *gigas* × *muricata*, all failures. The experiments of 1913, consisting of 75 trials on $m \times g$ and 30 trials on $g \times m$, were with plants heavily fertilized with bone meal, 1 kilogram to the square meter. The behavior of the inter- and back-crosses as far as I have studied them is given below.

(a and b) Double reciprocals

During two seasons (1912, 1916) I have attempted 47 times to make the cross $(g \times m) \times (m \times g)$ and 61 times to make the reverse double reciprocal $(m \times g) \times (g \times m)$ but without results. The hand-pollinated flowers failed to develop a single capsule.

(c) Sesquireciprocal, *gigas* × (*muricata* × *gigas*)

Pollinations of gigas from the F_1 *muricata* × *gigas*, in all 27 operations (1915, 1916), produced no capsules.

(d) Sesquireciprocal, (*gigas* × *muricata*) × *gigas*, culture 17.33

Pollinations in 1916 have given medium-sized capsules well filled with seed-like structures. A culture at date, March 1917, from the contents of 8 capsules in Petri dish presented after 6 weeks 74 seedlings, a germination of about 50 percent. The young rosettes show a wide range of variation and it is probable that the mature culture will exhibit a behavior similar to that described for the iterative (*muricata* × *gigas*) × *gigas*.

(e) Sesquireciprocal, *muricata* × (*gigas* × *muricata*)

No capsules were produced by this cross, 19 attempts in 1916.

(f) Sesquireciprocal, (*muricata* × *gigas*) × *muricata*, culture 16.32

This cross, 43 trials (1915, 1916), has always yielded full capsules with numerous seed-like structures. Sowings of the contents of 6 capsules in Petri dishes gave in 7-8 weeks 26 seedlings, the residue consisting of 538 empty seeds and 16 with contents; there were also some empty abortive structures and much ovule powder. The germination,

therefore, was very poor, 4.3 percent. The seedlings set in the earth developed no green in their cotyledons and died after 2 or 3 weeks.

(g) Iterative, *gigas* × (*gigas* × *muricata*)

This cross produced no capsules, 9 trials in 1916.

(h) Iterative, (*gigas* × *muricata*) × *muricata*, culture 17.34

Pollinations in 1916 gave medium-sized capsules well filled with seed-like structures. Only 2 seedlings appeared in a Petri dish culture after 6 weeks, March 1917, from the contents of 10 capsules, about 310 seed-like structures. The germination was therefore extremely low, .64 percent. The 2 seedlings developed no green in their cotyledons and promptly died, thus presenting a behavior similar to that of the sesquireciprocal (*muricata* × *gigas*) × *muricata*.

(i) Iterative, *muricata* × (*muricata* × *gigas*)

Pollinations of *muricata* from the F_1 *muricata* × *gigas* as in the case of the back-cross to the other parent, $g \times (m \times g)$, were fruitless; 61 attempts (1915, 1916) gave no capsules.

(j) Iterative, (*muricata* × *gigas*) × *gigas*, culture 16.31

This cross, 56 trials (1915, 1916), always gave well developed capsules with large seeds. From the contents of 3 capsules in a Petri dish there developed after 6 weeks 37 seedlings leaving a residue of 44 empty seeds, 9 seeds with contents, and numerous abortive structures grading into a large amount of ovule powder, a germination of 41 percent. Of the seedlings 36 survived giving a most varied assemblage of plants hardly two of which were alike. This culture was one of the most interesting that I have ever observed among hybrids of Oenothera. Evidently there is a very remarkable range in the structure of the female gametes of the F_1 *muricata* × *gigas* and extended genetical and cytological studies of this back-cross with the *gigas* parent should prove of exceptional interest.

(k) These crosses involving *muricata* and *gigas* so bristle with problems of sterility that discussion of our present data would not be justified. Since the *gigas* parent with 28 chromosomes has double the number present in *muricata*, and the F_1 hybrids are therefore triploid, we may with reason expect that some of the surprising results described above are bound up with irregularities of chromosome distribution.

SUMMARY

1. Data is presented in tables 1 and 2 showing the extent of delayed germination in earth-sown cultures as contrasted with the germination forced to completion under experimental conditions. It is not probable that the cultures here described, being from earth-sown seed, properly represented the possibilities of the viable seeds even though the pans were generally kept for at least 6 weeks.

2. The experimental tests of seed germination in Petri dishes showed some remarkably high degrees of seed sterility especially in the crosses involving *biennis* and *muricata* (table 1).

3. Some new types are added to the forms reported by DE VRIES for the inter- and back-crosses of the F_1 hybrids between *biennis* and *muricata* (page 169). The view is held by the writer that the relatively few types described among these hybrids represent a limited number of classes or segregates able to survive the extraordinarily high mortality among the gametes and zygotes.

4. A much greater variety of forms is found among the inter- and back-crosses of the F_1 hybrids between *biennis* and *Franciscana* where the amount of seed sterility is much less than in the crosses involving *biennis* and *muricata*, and this range of forms is interpreted as segregation.

5. The results for double reciprocals from F_1 hybrids of *biennis* and *grandiflora* also indicate a segregation of factors. Segregation in the F_2 generations from the same F_1 hybrid plants employed in making the double reciprocals was apparently masked by the low percentages of germination obtained from the earth-sown seeds. The presence of a remarkable class of dwarfs (fig. 6) was noted in all of these cultures.

6. Data on crosses involving *muricata* and *gigas* expose remarkable situations with problems of sterility in the foreground.

7. Remarkable linkage or correlations of characters were recorded especially for crosses in which *biennis* and *Franciscana* are concerned.

8. It appears to the writer doubtful whether the formulae presented by DE VRIES for the behavior of the inter- and back-crosses of the F_1 hybrids between *biennis* and *muricata* express a fundamental law. It seems more probable that the results of the formulae represent particular classes among a much larger number which either through delayed germination have not appeared in earth-sown cultures or through high degrees of sterility, both gametic and zygotic, are eliminated.

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FURTHER STUDIES ON THE RELATIONSHIP BETWEEN BILATERAL ASYMMETRY AND FERTILITY AND FECUNDITY IN THE UNILOCULAR FRUIT[1]

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INTRODUCTORY

In a paper appearing in an earlier number of GENETICS, I outlined (HARRIS 1916) the attempts which have hitherto been made to solve certain of the problems of the correlation between morphological and physiological characters by the application of quantitative methods to data from plant organisms, and gave series of measurements of degree of development in normal and variant seedlings. In this paper, I shall present the results of the analysis of 16 series of data for fertility in pods of the garden bean. These are supplementary to 53 series already published (HARRIS 1912 a).

While the nature of the problem is fully discussed in the memoir just cited, a simple explanation will serve the reader's convenience.

Externally a bean or pea pod is seen to have two sutures, the dorsal and the ventral. The pod splits most easily along the ventral suture and shows the seeds and the ovules which have ceased development at an early stage to be attached to the two margins just freed by the splitting. These two margins were free in the earlier stages of development. The pod may, therefore, be looked upon as a plate of tissue folded along the dorsal suture about which it is symmetrical or asymmetrical in respect of the number of ovules laid down upon its two margins. If the number be odd (3, 5, 7, etc.) the plate must have one ovule, at least, more on one side than on the other. If the number be even, the organ is most probably symmetrical, for an asymmetrical disposition of the ovules with respect of the central axis could only result from an excess of two ovules on one margin.

If the reader feels inclined to inquire why the discussions of the problem of the relationship of asymmetry and physiological capacity was

[1] Studies on the correlation between morphological and physiological characters. II.

not carried out on materials in which the degree of asymmetry could be expressed on a definite quantitative scale, the answer is very simple. Such measures are very difficult to secure. This is also true of any measure of physiological differentiation. Because of the slightness of variations in these characters and the reasonableness of supposing any relationship between them to be of a low order of magnitude, the number of measurements upon which any conclusion could be based would of necessity be very large indeed. Under these circumstances, it seems most desirable in preliminary work to use observations collected primarily for other purposes. Such data are available for a relatively large number (about a quarter of a million) of pods of garden beans, grown and counted in various genetical studies. Had the analysis of such available materials indicated the absence of any relationship between asymmetry and fecundity, it would be idle to urge the laborious collection of more accurately measured data for the specific purposes of the present problem. In view of the results which we have secured in the preliminary analysis of those collected incidentally, the justification of further studies of the same kind is quite clear.

MATERIALS AND METHODS

The first study of fertility in Phaseolus involved the pods secured in 53 cultures of dwarf varieties of garden beans, grown under a wide range of conditions in Kansas, Missouri, Ohio, and on Long Island.

The most comprehensive description of these materials is found in a memoir upon the influence of the starvation of the ascendants upon the characteristics of the descendants, but other information may be secured from a bibliography published elsewhere (HARRIS 1914).

The present investigation is based upon a lot of pods derived from 16 cultures, comprising 4 varieties, made on the grounds of the STATION FOR EXPERIMENTAL EVOLUTION in 1912. These were grown in the same field, hence under conditions of a high degree of uniformity as compared with the first 53 cultures. Details concerning the experimental conditions of this culture will eventually be published elsewhere. The ancestry of the plants and the history of the strains prior to 1912 may be obtained by substituting T for C in the formulae by which the cultures are designated, and referring to an earlier paper (HARRIS 1912 b).

The countings of number of ovules and seeds were made with great care by Miss EDNA LOCKWOOD, Miss MARGARET GAVIN and Miss LILLIE GAVIN, all of whom have had several years' experience in work of this

kind. This phase of the work was, I believe, carried out with greater accuracy than in our preceding series. That the results are altogether trustworthy cannot be urged. The determination of the number of abortive ovules is not always an easy task, and the boundary line between an abortive ovule and a perfectly developed seed is in many cases a purely arbitrary one. There are clear evidences of the existence of personal equation in the countings.

The data are, I believe, quite as accurate (at least) as those upon which genetic conclusions are generally based. They are the best we have been able to obtain up to the present, and have been secured and reduced at the cost of an enormous amount of labor. Until they can be replaced by others demonstrably superior, they may serve their purpose in indicating the nature of certain very obscure relationships. The closeness of agreement of the new data here presented with those due chiefly to other observers is one of the strongest evidences for a degree of accuracy sufficient for present requirements.

The correlation surfaces for number of ovules and number of seeds per pod are shown in the accompanying tables.

NHHT Series

Seeds per pod	Ovules per pod: 3	4	5	6	7	8	9	Totals
1	—	—	11	9	2	—	—	22
2	1	8	50	62	19	—	—	140
3	—	9	143	221	61	4	—	438
4	—	23	206	431	120	5	—	785
5	—	—	266	672	181	9	1	1129
6	—	—	—	674	250	14	1	939
7	—	—	—	—	230	29	—	259
8	—	—	—	—	—	10	—	10
	1	40	676	2069	863	71	2	3722

NHHHT Series

Seeds per pod	Ovules per pod: 3	4	5	6	7	8	9	Totals
1	—	3	13	27	8	—	—	51
2	2	14	108	137	53	2	—	316
3	3	43	250	433	116	10	—	855
4	—	51	479	756	213	10	—	1509
5	—	—	638	1295	324	19	—	2276
6	—	—	—	1461	466	26	—	1953
7	—	—	—	—	424	21	—	445
8	—	—	—	—	—	23	1	24
	5	111	1488	4109	1604	111	1	7429

NHDT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	Totals
1	—	—	5	5	3	—	13
2	1	4	18	34	15	1	73
3	—	7	66	87	39	2	201
4	—	9	102	146	66	5	328
5	—	—	125	266	68	11	470
6	—	—	—	266	125	10	401
7	—	—	—	—	87	15	102
8	—	—	—	—	—	12	12
	1	20	316	804	403	56	1600

NHDDT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	9	Totals
1	—	1	7	18	6	—	—	32
2	—	13	81	131	27	3	—	255
3	4	32	193	375	112	6	—	722
4	—	35	413	693	180	9	—	1330
5	—	—	535	1163	267	17	1	1983
6	—	—	—	1328	357	17	—	1702
7	—	—	—	—	354	15	—	369
8	—	—	—	—	—	14	1	15
	4	81	1229	3708	1303	81	2	6408

NDDT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	Totals
1	—	1	6	5	1	—	13
2	1	3	10	21	1	—	36
3	—	9	54	80	14	—	157
4	—	12	94	138	16	1	261
5	—	—	134	197	22	—	353
6	—	—	—	248	38	—	286
7	—	—	—	—	44	—	44
8	—	—	—	—	—	1	1
	1	25	298	689	136	2	1151

NDDDT Series

Ovules per pod

Seeds per pod	2	3	4	5	6	7	8	Totals
1	—	—	4	7	13	2	—	26
2	2	1	4	55	70	16	1	149
3	—	—	27	141	201	58	1	428
4	—	—	23	278	397	62	1	761
5	—	—	—	347	617	88	7	1059
6	—	—	—	—	778	150	4	932
7	—	—	—	—	—	140	4	144
8	—	—	—	—	—	—	2	2
	2	1	58	828	2076	516	20	3501

NDHT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	9	Totals
1	—	3	8	7	1	—	—	19
2	1	4	35	67	14	—	—	121
3	2	23	102	150	37	2	—	316
4	—	17	220	268	54	3	1	563
5	—	—	274	427	72	2	—	775
6	—	—	—	546	82	4	—	632
7	—	—	—	—	86	4	—	90
	3	47	639	1465	346	15	1	2516

NDHHT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	Totals
1	—	1	8	7	5	—	21
2	1	9	49	73	11	1	144
3	—	18	135	183	42	4	382
4	—	34	288	373	68	4	767
5	—	—	395	633	86	3	1117
6	—	—	—	755	104	5	864
7	—	—	—	—	107	7	114
8	—	—	—	—	—	3	3
	1	62	875	2024	423	27	3412

USHT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	Totals
1	1	16	56	77	13	—	163
2	5	13	144	162	21	—	345
3	3	45	231	272	35	—	586
4	—	43	411	369	45	1	869
5	—	—	467	549	72	—	1088
6	—	—	—	590	71	2	663
7	—	—	—	—	52	3	55
8	—	—	—	—	—	3	3
	9	117	1309	2019	309	9	3772

USHHT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	Totals
1	2	10	44	47	9	—	112
2	4	17	110	141	18	—	290
3	1	28	158	233	34	1	455
4	—	26	308	307	30	2	673
5	—	—	418	503	40	1	962
6	—	—	—	490	55	—	545
7	—	—	—	—	48	2	50
	7	81	1038	1721	234	6	3087

USDT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	Totals
1	2	8	63	51	5	—	129
2	7	8	110	130	20	—	275
3	2	48	151	146	28	—	375
4	—	44	299	240	22	—	605
5	—	—	425	335	33	1	794
6	—	—	—	347	38	—	385
7	—	—	—	—	37	1	38
	11	108	1048	1249	183	2	2601

USDDT Series

Ovules per pod

Seeds per pod	2	3	4	5	6	7	8	Totals
1	—	1	11	59	77	8	—	156
2	1	8	25	144	209	32	—	419
3	—	4	62	269	293	50	2	680
4	—	—	65	447	464	45	—	1021
5	—	—	—	533	689	71	—	1293
6	—	—	—	—	642	69	—	711
7	—	—	—	—	—	75	—	75
	1	13	163	1452	2374	350	2	4355

FSHT Series

Ovules per pod

Seeds per pod	4	5	6	7	8	Totals
1	1	27	42	24	2	96
2	2	53	137	63	3	258
3	8	88	219	115	6	436
4	12	126	322	163	7	630
5	—	145	451	185	8	789
6	—	—	508	200	7	715
7	—	—	—	188	9	197
8	—	—	—	—	6	6
	23	439	1679	938	48	3127

FSHHT Series

Ovules per pod

Seeds per pod	3	4	5	6	7	8	9	Totals
1	—	2	20	39	31	1	—	93
2	1	1	53	137	90	4	—	286
3	1	8	68	270	142	13	—	502
4	—	2	134	327	190	6	—	659
5	—	—	204	600	230	12	—	1046
6	—	—	—	562	269	8	—	839
7	—	—	—	—	244	17	—	261
8	—	—	—	—	—	13	—	13
9	—	—	—	—	—	—	1	1
	2	13	479	1935	1196	74	1	3700

FSDT Series

Seeds per pod	Ovules per pod: 3	4	5	6	7	8	9	Totals
1	1	2	15	30	11	1	—	60
2	1	6	41	122	60	7	—	237
3	—	5	80	171	100	7	—	363
4	—	4	96	244	117	13	—	474
5	—	—	107	335	152	13	—	607
6	—	—	—	377	192	16	1	586
7	—	—	—	—	185	12	—	197
8	—	—	—	—	—	7	—	7
	2	17	339	1279	817	76	1	2531

FSDDT Series

Seeds per pod	Ovules per pod: 2	3	4	5	6	7	8	9	Totals
1	1	—	1	16	35	19	—	—	72
2	—	—	6	57	125	61	3	—	252
3	—	—	11	80	231	119	10	—	451
4	—	—	10	155	377	145	8	—	695
5	—	—	—	231	604	217	8	—	1060
6	—	—	—	—	693	268	11	—	972
7	—	—	—	—	—	260	17	1	278
8	—	—	—	—	—	—	6	—	6
	1	—	28	539	2065	1089	63	1	3786

Two methods of comparing the capacity for seed production of asymmetrical ("odd") and probably symmetrical ("even") pods have been employed. First, the simple ratios of the total number of seeds matured to the total number of ovules laid down has been computed for both types of pod. In comparison, $F_o - F_e$ gives the sign and the magnitude of the difference in the two coefficients of fertility. Thus for series NHHHT the results are:

For "odd" pods, total ovules = 18692,
total seeds = 14804,
$14804/18692 = .79199 = F_o$
For "even" pods, total ovules = 25986,
total seeds = 20885,
$20885/25986 = .80370 = F_e$
$F_o - F_e = .79199 - .80370 = -.01171$

Second, the average deviations of the empirical mean number of seeds matured for each number of ovules formed per pod from the theoretical mean number due to a regression equation based on the whole population has been computed for both "odd" and "even" pods, as they will be called for the sake of convenience.

The only problem to be solved in the use of this method is the selection of the regression equation to be employed. Because of its very

general validity and the ease with which it may be computed, the straight line equation

$$s = (\bar{s} - r_{os}\frac{\sigma_s}{\sigma_o}\bar{o}) + r_{os}\frac{\sigma_s}{\sigma_o}o$$

where the bars denote means and the sigmas the standard deviations of the two variables, o = ovules and s = seeds per pod whose correlation is measured by r, must first be tested.

As in the first paper, the linear equation is the only one used.

To meet the possibility that there may be geneticists unfamiliar with the arithmetical processes employed, they may be illustrated on series NHHHT.

The correlation coefficients may be most advantageously determined by a method giving the total number of seeds produced by pods of each ovule grade (HARRIS 1910). Thus:

Ovules per pod	Number of pods	Total seeds in pods
3	5	13
4	111	364
5	1488	6085
6	4109	19865
7	1604	8698
8	111	656
9	1	8

$N = 7429, \quad \Sigma(os) = 217316, \quad \Sigma(os)/N = 29.252385$

For ovules:

$\Sigma(o) = 44678, \quad \Sigma(o)/N = 6.013998, \quad \mu_2 = .542820$

$\Sigma(o^2) = 272726, \quad \Sigma(o^2)/N = 36.710992, \quad \sigma_o = .736763$

For seeds:

$\Sigma(s) = 35689, \quad \Sigma(s)/N = 4.804010 \quad \mu_2 = 1.649307$

$\Sigma(s^2) = 183703, \quad \Sigma(s^2)/N = 24.727819, \quad \sigma_s = 1.284253$

Whence

$$r_{os} = \frac{\Sigma(os)/N - \bar{o}\bar{s}}{\sigma_o \sigma_s} = \frac{29.252385 - 6.013998 \times 4.804010}{.736763 \times 1.284253} = .381613$$

In terms of regression we have

$$s = (\bar{s} - r\frac{\sigma_s}{\sigma_o}\bar{o}) + r\frac{\sigma_s}{\sigma_o}o$$

or, substituting constants,

$$s\ (= 4.804010 - .381613\ \frac{1.284253}{.736763}\ 6.013988) + .381613\ \frac{1.284253}{.736763}\ o$$

the final result is

$$s = .803558 + .665190\ o$$

For the calculation of η we have

Ovules per pod	Number of pods	$\bar{s}_x - \bar{s}$	$(\bar{s}_x - \bar{s})^2$
3	5	−2.20401	4.85766
4	111	−1.52473	2.32480
5	1488	− .71463	.51069
6	4109	+ .03050	.00093
7	1604	+ .61868	.38277
8	111	+1.10590	1.22301
9	1	+3.19599	10.21435

$$s\,[n_x(\bar{s}_x - \bar{s})^2] = 1806.00073$$

$$\eta^2 = \frac{s\,[n_x(\bar{s}_x - \bar{s})^2]/N}{\sigma_s^2} = \frac{.243101}{1.649307},\quad \eta = .3839$$

Blakeman's (1906) test is given by

$$\eta^2 - r^2 = .001767,\quad \sqrt{\eta^2 - r^2} = \sqrt{\zeta} = .042043$$

whence

$$\frac{\frac{1}{2}\sqrt{\zeta}}{\chi_1} = 2.686$$

Calculating the theoretical or smoothed means from the regression equations

$$s = .803558 + .665190\ o$$

and comparing with the empirical means

Ovules per pod	Number of pods	Average seeds $\bar{s}_x$	Calculated average seeds $\bar{s}_x'$	Average seeds less calculated average seeds $\bar{s}_x - \bar{s}_x'$
3	5	2.60000	2.79913	− .19913
4	111	3.27928	3.46432	− .18504
5	1488	4.08938	4.12951	− .04013
6	4109	4.83451	4.79470	+ .03981
7	1604	5.42269	5.45989	− .03720
8	111	5.90991	6.12508	− .21517
9	1	8.00000	6.79027	+1.20973

Summing the product of the deviations of these empirical means from the theoretical straight lines due to the equations by the numbers of pods upon which they are based, I find

For even pods, +119.16031,
For odd pods, —119.15566,

or since there are 3098 odd pods the mean deviation of the asymmetrical class is

—.0384

RESULTS

The accompanying table contains the fundamental constants upon which discussions must be based.

The magnitude of the relationship between the number of ovules formed and the number of seeds developing per pod is shown by the correlation coefficients in the first column, by the correlation ratios in the second column, and by the second constant of the regression straight line equations in the fourth column following the key letters. The closeness of agreement of the several series is shown by the regression lines which have been drawn for all the series in diagram 1.

Consider first of all the nature of the change in the mean number of seeds matured per pod associated with variations in the number of ovules per pod.

The distribution of the empirical means around the regression straight line is shown for four of the series in diagram 2.

The ratio of $\frac{1}{2}\sqrt{\zeta}$ of BLAKEMAN'S test for linearity (BLAKEMAN 1906) to the χ_1 of Miss GIBSON'S tables (1906) appears in the third column of the table.

To be considered as indicating strictly linear regression, i.e., a uniform rate of change in mean number of seeds per pod, the value of $\frac{1}{2}\sqrt{\zeta}\,/\,\chi_1$ should not exceed 2.5. The entries in the third column show that it does as a matter of fact exceed this value in 13 out of the 16 cases.

Thus regression cannot, by formal tests, be considered linear. Two points must, however, be taken into account. First, if there be a relationship between the bilateral asymmetry of the ovary and its capacity for maturing its ovules into seeds, strictly linear regression cannot obtain. Second, one single type of equation is desirable for comparative studies,—at least, for those of a preliminary nature. Since the straight line equation was the one employed in the first series of determinations

Series	Coefficient of correlation, r	Correlation ratio, η	$\frac{1}{2}\sqrt{5}$ / χ_1	Regression equation	Mean deviation of odd	$F_o - F_e$
HHT	.4177	.4195	1.757	$s = +.3863 + .7301\ o$	—.0421	—.01281
HHHT	.3816	.3839	2.686	$s = +.8035 + .6651\ o$	—.0384	—.01171
HDT	.3818	.3873	1.919	$s = +.8884 + .6373\ o$	—.0882	—.02558
HDDT	.3624	.3657	2.896	$s = +.9608 + .6413\ o$	—.0304	—.00909
DDT	.3814	.3825	7.142	$s = +.5519 + .7112\ o$	+.0274	+.01290
DDDT	.3677	.4466	11.120	$s = +.7797 + .6712\ o$	—.0665	—.01408
DHT	.3307	.3435	3.462	$s = +1.1866 + .5954\ o$	—.0736	—.01182
DHHT	.3343	.3445	3.599	$s = +1.2441 + .5950\ o$	—.0885	—.01309
USHT	.2943	.3019	3.046	$s = +.7972 + .6034\ o$	—.0258	+.00521
USHHT	.2760	.2860	3.086	$s = +.9933 + .5763\ o$	—.0091	+.01484
USDT	.2597	.2648	1.963	$s = +1.2248 + .5231\ o$	—.0018	+.02189
USDDT	.2818	.2877	2.844	$s = +1.0344 + .5623\ o$	—.0153	+.01170
FSHT	.2489	.2590	2.960	$s = +1.2488 + .5280\ o$	—.0956	—.03840
FSHHT	.2274	.2357	2.808	$s = +1.6355 + .4757\ o$	—.0625	—.03364
FSDT	.2937	.3030	2.777	$s = +.7971 + .6012\ o$	—.0170	—.01164
FSDDT	.2744	.2808	2.710	$s = +1.3101 + .5517\ o$	—.0546	—.02605

it seems desirable to use it here as well, especially in view of the fact that it is not yet demonstrated that any other single equation would prove more effective in smoothing the empirical means.[2]

Turn now to the two measures of the capacity of the two types of pods for seed production. These are given in the two final columns of the table.

In presenting these results I shall first give those derived from the sixteen new experiments, here presented for the first time. I shall then combine with these the fifty-three series already published. Thus the present paper not only forms a contribution of a large mass of new material, but summarizes the whole of the available data.

Considering the signs only of the constants measuring the relationship between asymmetry and capacity for seed production, it is clear that with a single exception the regression line method indicates lower fertility in the asymmetrical pods. The results are not so concordant in the case of the method of differences in coefficients of fertility, for here 5 out of the 16 series show a lower fecundity in the more symmetrical class of pods.

[2] The actual data are published and at the disposal of anyone who feels inclined to fit regression curves of a higher order. Personally, I feel that the time required would be better employed on the biological rather than the statistical side of the problem.

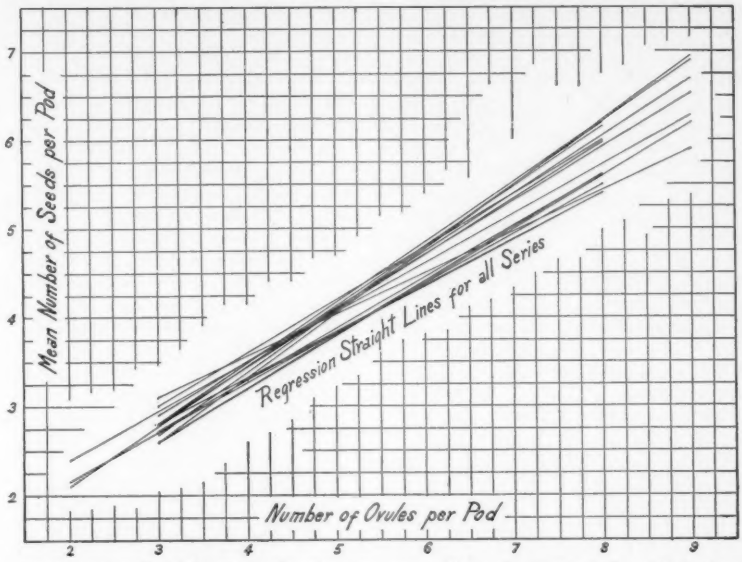

DIAGRAM 1.—Straight lines showing the regression of number of seeds matured upon number of ovules formed per pod in 16 cultures of Phaseolus.

In the sets of observations already published there were by both methods 35 series in which the asymmetrical pods showed a lower capacity for maturing their ovules into seeds as compared with 18 in which they showed a higher capacity. This comparison is of course based on signs only. An analysis of the results on the basis of the magnitudes of the coefficients will be made presently.

Considering all the constants available up to the present time, it is clear that as analyzed by the regression line method there are 50 series in which the asymmetrical pods show a smaller capacity for maturing their ovules into seeds as compared with 19 in which they show a higher capacity. If conclusions be drawn from the coefficient of fecundity method, the results are in practical agreement. Thus 46 of the 69 series show a lower capacity for maturing ovules into seeds in the asymmetrical pods.

These are rather wide deviations from the equality which one would expect if there were no biological cause for differences in the fertility of the two classes of pods, i. e., if the differences observed were due purely and simply to the probable errors of random sampling. If such

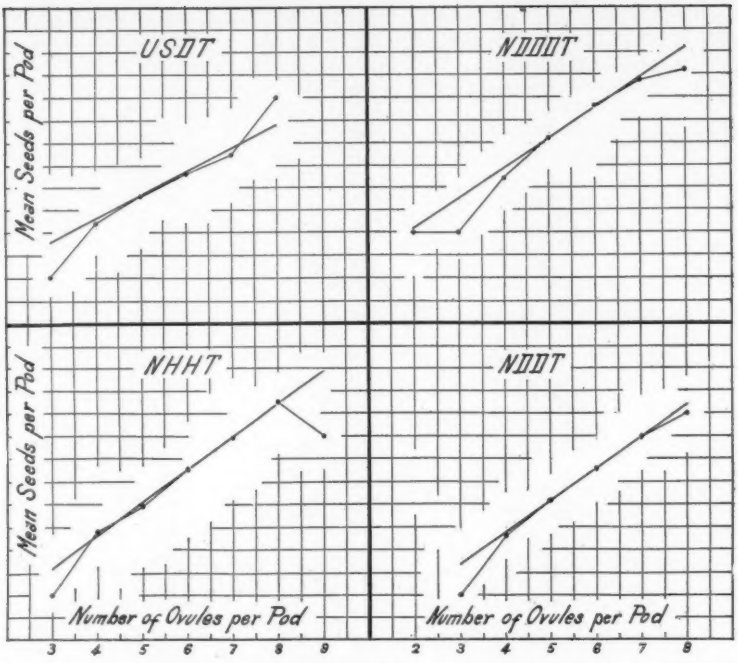

DIAGRAM 2.—Regression straight lines with empirical mean numbers of seeds per pod in four series of Phaseolus.

were the origin of the observed differences in the fecundity of the two classes of pods, there should be, within the limits set by the probable error of random sampling given by

$$.67449\sqrt{69\times.5\times.5}$$

an equal division into two groups in one of which the symmetrical and in the other of which the asymmetrical is the more fertile. The actual deviation of the observed number of positive and negative coefficients from equality is,

For the regression line method

$$50 - 34.5 = 15.5 \pm 2.80$$

For the coefficient of fertility method

$$46 - 34.5 = 11.5 \pm 2.80$$

These deviations from equality are about 5.5 and 4.1 times as large as

their probable errors and must, therefore, be looked upon as probably significant.

The results by the regression line method are so uniform throughout that it is difficult to discuss the closeness of agreement of this and the coefficient of fecundity method on the new materials. Combining the present series with those previously published, we have the results set forth in the accompanying table.

Coefficient of fertility method

Regression line method	+	−	Totals
+	15	4	19
−	8	42	50
Totals	23	46	69

Thus the two methods, which do not necessarily give identical results, are in very close agreement indeed. Series which are classified as showing a negative relationship by one method will in the great majority of instances—in 57 of the 69 available cases—show the same relationship when classified by the other method. Were the two methods employed not thus consistent, no confidence whatever could be placed in the results. That they are not in universal agreement is due to the fact that no single method of analyzing the data so far known is without some objectionable feature.

A comparison of the two methods of determining the relationship between bilateral asymmetry and the capacity of the ovary for maturing its ovules into seeds, which takes into account the magnitudes of the constants, instead of their signs merely, may best be made by determining the correlation between them. This is found to be

$$r = .8577,$$

a value indicating a very close agreement indeed. The relationship is represented graphically in diagram 3 in which the closeness of agreement is shown by the slope of a straight line representing the regression equation deduced from the correlation coefficient. The solid dots show the position with reference to the two general means and the regression straight line of both constants for the 69 individual series. The shaded areas show the magnitude of the deviation of the two general means for the two methods of measurement from the zero which would be

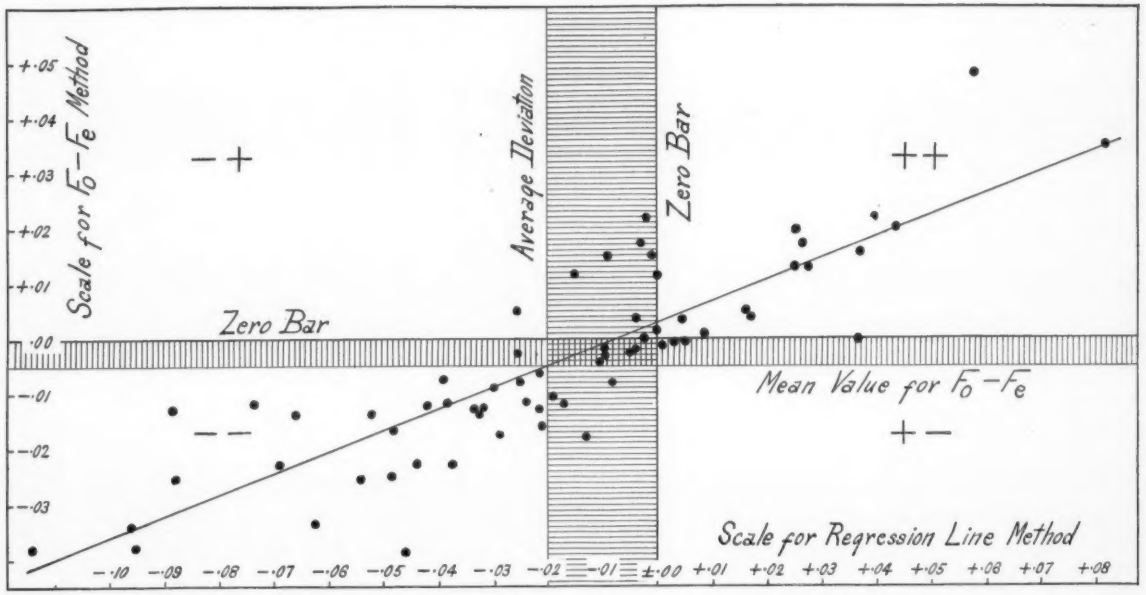

DIAGRAM 3.—Scatter diagram showing the agreement between the two methods used in computing the capacity for seed production of symmetrical and asymmetrical pods. The solid dots show on the two scales the actual values obtained by the two methods. The shaded areas show the extent of the deviations of the means of the two sets of results from zero. The straight line represents, in terms of regression, the correlation between the results of the two methods.

expected as the average of the constants if there were no difference in the capacity of the two types of pods for maturing their ovules into seeds.

One of the strongest evidences for the validity of the conclusions concerning a negative relationship between bilateral asymmetry with respect of ovule number and capacity for seed production is the consistency of results obtained at different times with series of materials which in many ways are quite dissimilar. The results have been worked up in four lots as the data have accumulated. These series have been counted, tabled and analyzed at periods several years apart. Classifying the data into these purely arbitrary groups, the results for the signs of the coefficients measuring the capacity for seed production of asymmetrical pods are as follows:

By the regression line method:

Lot 1. 20 series, 15 negative and 5 positive,
Lot 2. 20 series, 12 negative and 8 positive,
Lot 3. 13 series, 8 negative and 5 positive,
Lot 4. 16 series, 15 negative and 1 positive.

By the method of comparison of coefficients of fecundity:

Lot 1. 20 series, 14 negative and 6 positive,
Lot 2. 20 series, 12 negative and 8 positive,
Lot 3. 13 series, 9 negative and 4 positive,
Lot 4. 16 series, 11 negative and 5 positive.

Such uniformity of results can hardly be due to chance. It indicates the existence of a real biological relationship between asymmetry and capacity for seed production.

Series	Regression line method		$F_o - F_e$ method		Totals
	Negative	Positive	Negative	Positive	
Navy (H)	9	4	10	3	13
Navy (D)	9	4	10	3	13
Burpee's Stringless (G)	5	3	6	2	8
Ne Plus Ultra (U)	10	5	3	12	15
White Flageolet (F)	14	1	14	1	15
Golden Wax (L)	3	0	3	0	3
Black Wax (BW)	0	2	0	2	2
Totals	50	19	46	23	69

As another check upon our conclusions, the constants for all available series may be classified by varieties, as in the table immediately above.

Note that in every variety with the exception of Ne Plus Ultra and Black Wax (in which the materials were very unsatisfactory) the relationships are of the same general kind.

Turning to averages as a means of closer analysis, I find the following results for the 16 new series. The constants obtained from the 53 series investigated some years ago are added for comparison and the averages based on all the available data are laid beside the others.

Regression line method,

New series	—.0426
Earlier series	—.0139
All series	—.0202

Coefficient of fecundity method,

New series	—.0088
Earlier series	—.0040
All series	—.0051

If instead of giving the constants for the 69 series equal weight in determining their average value, they be loaded with the number of asymmetrical pods upon which they are based, the results are as follows:

Regression line method,

New series	—.0428
Earlier series	—.0125
All series	—.0191

Coefficient of fecundity method,

New series	—.0096
Earlier series	—.0037
All series	—.0050

Thus the average values of the constants, as well as the distribution with regard to signs, indicate a lower capacity for seed development in the bilaterally asymmetrical pods.

By both methods the magnitudes of the differences are larger in the second series of determinations than they are in the first. This is the result which one would expect if there be a negative relationship between asymmetry and capacity for seed production and if the second series of determinations is technically the better of the two.

The question naturally arises: Why, if there be really a negative relationship between morphological asymmetry and physiological capacity, do a certain number of the coefficients show a positive correlation between these two variables, i. e., indicate that the asymmetrical pods are more capable of carrying out their physiological functions than the symmetrical?

There may be biological factors not yet fully investigated underlying this phenomenon, but I think it is due chiefly to the slightness of the relationship under investigation and the difficulty of obtaining samples of data adequately large and sufficiently free from error to demonstrate the general law in each individual instance. For two reasons large differences should not be expected between the fertility of symmetrical and asymmetrical ovaries. First, the actually existing asymmetry in these cases is not large. Second, the correlation between somatic characters and fertility is (as I have shown in papers which need not be cited here) generally low.

In such delicate interdependencies, there is always the possibility that the errors of sampling may give even a false sign to a constant based upon samples of the size that one is ordinarily able to secure in biological work. In any series of determinations one must, therefore, expect a number of the constants to bear positive signs, even though the actual biological relationship in an infinitely large population may be a negative one.

RECAPITULATION

The foregoing pages present the results of the statistical reduction of data bearing on the problem of the relationship between bilateral asymmetry with respect of number of ovules produced on the two carpellary margins and the capacity for seed production of the unilocular fruit.

Primarily, they set forth the constants derived from the data of 16 hitherto unanalyzed series of garden beans, comprising a total of 56698 pods. Secondarily, they give the results of comparison and combination with the constants from 53 series comprising 166136 pods published in 1912.

The constants of either of these lots of data taken independently may be considered to establish the conclusion that there is a negative relationship between bilateral asymmetry and the capacity of the pod for maturing its ovules into seeds.

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ON THE APPLICABILITY OF PEARSON'S BISERIAL r TO THE PROBLEM OF ASYMMETRY AND FERTILITY IN THE UNILOCULAR FRUIT

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INTRODUCTORY

When PEARSON (1909) published his formula for measuring the intensity of relationship between an alternative and a quantitatively measured variable, it was quite clear that the method might be used in certain problems of fertility and fecundity which had then been under investigation for several years. In preparing a first paper on these studies (HARRIS 1912) it seemed desirable to forego the application of correlation methods to the problem until the formula had been somewhat more widely tested in practical work. The present paper proposes to illustrate the applicability of this method, unfortunately little used by biologists, to the problem of the relationship between bilateral asymmetry and capacity for seed production in the unilocular fruit.

Beyond any value which it may have as indicating biological applications for a valuable but as yet little recognized formula, the paper is solely a contribution to the further analysis of data presented elsewhere (HARRIS 1912, 1917 a).

It may be said at the outset that while correlation formulae are not essential for the demonstration of the existence of relationships of the kind under investigation, their application does allow of the measurement of the intensity of the interrelationship on a quantitative scale. Their use marks, therefore, the transition from relatively qualitative to relatively quantitative work.

METHODS

The method of analysis here employed is in essence very simple. Let r_{ao} be the correlation between asymmetry and number of ovules laid down, r_{as} the correlation between asymmetry and number of seeds matured. Now the values of r_{as} will be to some extent influenced by

[1] Studies on the correlation between morphological and physiological characters. III.

these of r_{ao}, since r_{os}, the correlation between number of ovules and number of seeds per pod, has always (in Phaseolus) been found to have a substantial positive value. To obtain a measure of the correlation between asymmetry and number of seeds produced *free from the influence of the correlation between asymmetry and number of ovules,* the well known partial correlation formula for three variables has been employed.

The only assumption necessary in the application of the biserial r is that the alternative character *is normal* in its frequency distribution. While asymmetrical and symmetrical, as measured by the "odd" or "even" number of ovules formed, must formally be regarded as truly discontinuous, they cannot be so considered fundamentally. Number of ovules while nominally a discrete variate is in reality dependent upon a large number of antecedent proximate causes, physiological and morphological, which are essentially continuous in their influence. Whether these shall produce an odd or an even number of ovules depends in all probability upon purely quantitative differences in the weight of these factors. For the great majority of practical purposes such variations may be considered to follow the normal or Laplace-Gaussian law.

Thus all that we require for the expression of the results for the 69 series of Phaseolus for which data on the number of ovules formed and the number of seeds matured per pod are now available, on as nearly as possible a truly quantitative scale is the 138 correlation coefficients for asymmetry and ovule and seed numbers, the 69 correlation coefficients for number of ovules and seeds, and the 69 partial correlations between asymmetry and number of seeds for constant number of ovules per pod.

It may be useful to illustrate the processes. In the simple formulae

$$r_{ao} = \frac{(\bar{o}_a - \bar{o})/\sigma_o}{z/f}, \quad r_{as} = \frac{(\bar{s}_a - \bar{s})/\sigma_s}{z/f}$$

$\bar{o}_a$, $\bar{s}_a$ indicate the mean number of ovules and seeds in asymmetrical pods, $\bar{o}$, $\bar{s}$, the mean number of ovules and seeds in all pods, σ_o, σ_s the standard deviations of number of ovules and seeds in the population at large. Thus the evaluation of the numerator is very simple indeed, consisting merely in the determination of the ratio of the deviation of the mean of the selected class from the population mean to the population standard deviation. Note that the sign of the correlation coefficient is given at once by $\bar{o}_a - \bar{o}$, $\bar{s}_a - \bar{s}$.

The value of the denominator must be determined from SHEPPARD'S tables of the probability integral (SHEPPARD 1902).

The necessary constants may be obtained in either of two ways. An illustration of the actual arithmetic may be useful to those who would like to follow the work in detail.

For series NHHHT

$$\tfrac{1}{2}(1-\alpha) = 3098/7429 = .4170144$$
$$\tfrac{1}{2}(1+\alpha) = 4331/7429 = .5829856$$
$$\alpha = .1659712$$

SHEPPARD'S tables I-II (II of PEARSON'S volume) give for the lower value of $\tfrac{1}{2}(1+\alpha)$

$$\tfrac{1}{2}(1+\alpha) = .5792597, \quad \Delta = .0039065$$

Hence

$$\theta = (.5829856 - .5792597)/.0039065 = .95377$$
$$\theta(1-\theta)/2! = .04409$$

The values of z corresponding to $\tfrac{1}{2}(1+\alpha) = .5792579$ in SHEPPARD'S tables are

$$z = .3910427, \quad \Delta = .0008008, \quad \Delta^2 = .0000373$$

Whence by the advancing difference formula

$$u = u_o + \theta\Delta u_o - \frac{\theta(1-\theta)}{2!}\Delta^2 u_o$$

$$z = .3910427 - (.95377 \times .0008008) + (.02205 \times .0000373) = 3902797$$

Using table III we have

$$\alpha = .16, \quad z = .3908939, \quad \Delta = .0010415, \quad \Delta^2 = .0000641$$
$$\theta = .59712, \quad \frac{\theta(1-\theta)}{2!} = .12028$$

Whence by the advancing difference formula

$$z = .3908939 - (.59712 \times .0010415) + (.12028 \times .0000641) = .3902796$$

a value differing by only 1×10^{-7} from that derived from SHEPPARD'S tables I-II, notwithstanding the small number of decimals retained in clearing the formulae.

RESULTS

The values of r_{os}, r_{ao}, and r_{as}, which are essential for the determination of the partial correlations between asymmetry and number of seeds matured for constant numbers of ovules per pod, are given in the first three columns of the accompanying table.

The values of r_{os} are treated in sufficient detail in a forthcoming paper (HARRIS 1917 b). Researches which may facilitate the interpretation of

the values of r_{ao} and r_{as} are still in progress. They will not, therefore, be discussed in this paper, further than to point out that both are preponderantly negative in sign, i. e., that as a rule a lower number of both ovules and seeds is associated with asymmetry.

The values of ${}_{o}r_{as}$ are distributed between positive and negative in the ratio 19 : 50. Thus they show a deviation of 15.5 ± 2.80 from an equality of division into positive and negative coefficients. Since the number of negative partial correlation coefficients is distinctly greater than the number of positive ones, the asymmetrical pods are relatively as well as absolutely less fertile than the symmetrical ones.

The values of ${}_{o}r_{as}$ are generally low. They range from —.0996 to +.0817, with a general average of —.0185. The average for the 19 positive partial correlations is +.0269 as compared with —.0358 for the 50 negative coefficients. Thus there is not merely a negative general average, but the average magnitude of the coefficients which are negative in sign is numerically larger than that of those which are positive in sign.

The results may now be compared with those secured in the other

Series	r_{os}	r_{ao}	r_{as}	${}_{o}r_{as}$
L	.3740	—.0254	—.0204	—.0118
LL	.3567	—.1932	—.0717	—.0030
LG	.1070	+.2373	—.0321	—.0595
BW	.1766	—.0327	+.0746	+.0817
BW_2	.1281	—.0286	+.0395	+.0425
G	.5420	—.0106	—.0313	—.0303
GG	.2469	—.0163	—.0221	—.0187
GGH	.4611	—.0301	—.0237	—.0110
GGH_2	.5167	—.1173	—.0559	+.0055
GGHH	.4891	—.1265	—.0901	—.0326
GGD	.3616	+.0952	+.0390	+.0050
GGD_2	.4257	—.0388	—.0503	—.0374
GGDD	.3863	+.1547	+.0998	+.0439
H	.4444	—.3451	—.1394	—.0167
HH	.5109	—.2781	—.1420	+.0002
HHC	.5037	—.3212	—.1286	+.0405
HHT	.4177	+.0806	—.0013	—.0387
HHH	.4257	—.3780	—.1882	—.0325
HHHC	.5007	—.2505	—.1429	—.0208
HHHT	.3816	+.0284	—.0212	—.0346
HD	.4178	+.1444	+.0766	+.0181
HDC	.5094	—.2518	—.1677	—.0474
HDT	.3819	+.0273	—.0605	—.0768

Series	r_{os}	r_{so}	r_{as}	$_{o}r_{as}$
HDD	.4999	—.0116	—.0119	—.0070
HDDC	.4635	—.4016	—.1994	—.0163
HDDT	.3625	+.0234	—.0164	—.0267
D	.5214	—.0075	—.0335	—.0346
DD	.4963	+.2423	+.1118	—.0100
DDC	.4633	—.4944	—.2279	+.0015
DDT	.3815	—.2921	—.0895	+.0248
DDD	.4437	+.3536	+.1608	+.0046
DDDC	.4292	—.4401	—.2362	—.0582
DDDT	.3678	—.1761	—.1182	—.0637
DH	.5476	—.2571	—.1315	+.0114
DHC	.4094	—.4939	—.2244	—.0280
DHT	.3307	—.2324	—.1370	—.0655
DHH	.4462	—.3183	—.1466	—.0054
DHHC	.4375	—.4420	—.2333	—.0494
DHHT	.3343	—.2882	—.1694	—.0809
USC	.3309	—.5046	—.1665	+.0007
USS	.5050	—.2408	—.1384	—.0194
USSC	.3319	—.4800	—.1366	+.0274
USH	.4700	—.1736	—.0552	+.0299
USHC	.3224	—.4644	—.1510	+.0014
USHT	.2944	—.4802	—.1614	—.0240
USHH	.3658	—.4046	—.1192	+.0310
USHHC	.3182	—.3697	—.1417	—.0273
USHHT	.2761	—.5244	—.1517	—.0085
USD	.3762	+.0140	—.0224	—.0299
USDC	.2447	—.4542	—.0559	+.0640
USDT	.2597	—.5031	—.1322	—.0018
USDD	.3697	+.1834	+.0319	—.0392
USDDC	.3153	—.4512	—.1453	—.0036
USDDT	.2818	—.4487	—.1383	—.0138
FSC	.3444	+.1691	+.0017	—.0611
FSS	.3672	—.0041	—.0423	—.0439
FSSC	.4115	+.1689	+.0264	—.0480
FSH	.4580	—.3819	—.1832	—.0100
FSHC	.2684	+.0706	—.0650	—.0874
FSHT	.2490	+.2948	+.0024	—.0767
FSHH	.3982	—.5785	—.2653	—.0466
FSHHC	.3247	+.0086	—.0629	—.0694
FSHHT	.2274	+.3221	+.0247	—.0527
FSD	.4332	—.0465	—.0242	—.0046
FSDC	.2665	+.0625	—.0791	—.0996
FSDT	.2937	+.2709	+.0667	—.0139
FSDD	.4212	—.0633	+.0287	+.0612
FSDDC	.3284	+.0237	—.0596	—.0714
FSDDT	.2745	+.2710	+.0325	—.0452

two methods of analysis. This may be most conveniently done by means of the correlation coefficient.

The results are:

For ${}_{o}r_{as}$ and $F_o - F_e$ method

$$r = .850 \pm .023$$

For ${}_{o}r_{as}$ and mean deviation from regression straight line method

$$r = .986 \pm .002$$

The straight line regression equation is shown for the mean deviation method and the ${}_{o}r_{as}$ method in diagram 1. Here the actual constants secured by the two methods are indicated by solid dots. The shaded areas show the amount of deviation of the means from zero which would be expected if there were no relationship between asymmetry and capacity for seed production.

It is unnecessary to represent the relationship between the results of ${}_{o}r_{as}$ and the F_o—F_e method graphically, since the correlation between the partial correlations and the mean deviations is so close that the graph already published for the mean deviation and the F_o—F_e method (HARRIS 1917 a, diagram 3) is, for all practical purposes, identical with it.

RECAPITULATION

In earlier papers it has been shown that there is a negative correlation between bilateral asymmetry in the unilocular fruit of Phaseolus and its capacity for maturing its ovules into seeds, asymmetrical fruits being less capable of seed development than symmetrical.

While the two proofs of the existence of the relationship there employed are quite valid, they do not express the intensity of the correlation on the universally comparable scale of —1 to +1. This has been the purpose of the present paper.

PEARSON's bi-serial r has been shown to be a suitable constant for measuring the correlation between asymmetry and actual numbers of ovules and seeds per pod. The influence of the correlation between the number of ovules and the number of seeds per pod upon the correlation between asymmetry and the number of seeds matured has been eliminated by the use of the partial correlation formula for three variables, one of which is constant.

The results are, therefore, expressed in terms of the partial correla-

DIAGRAM 1.—Correlation between deviation from regression straight line method and partial correlation method of measuring relationship between asymmetry and capacity for seed production.

tion between asymmetry and number of seeds matured for constant number of ovules per pod.

The constant is found to be of a very low order. The average value of $_{o}r_{as}$ for the 69 series of Phaseolus now available is about —.020.

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